

Systematics and biogeography of Colletinae with revisionary studies of the species  
of *Colletes* Latreille (Hymenoptera: Colletidae: Colletinae) from Chile and  
eastern South America

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## Abstract

The bee subfamily Colletinae (Hymenoptera: Colletidae) includes *c.* 545 valid species, the majority of which (*c.* 520 species) belong to the megadiverse *Colletes* Latreille. The genus-level placement of the other 25 species has been controversial, with the number of recognized genera varying considerably among authors. For this reason, the first major objective of this dissertation is to construct a morphological phylogeny based on maximum parsimony analyses to settle a long-standing controversy pertaining to the systematics of Colletinae. Results suggest that the following four genera should be recognized: *Colletes*, *Hemicotelles* Toro & Cabezas, *Mourecotelles* Toro & Cabezas and *Xanthocotelles* Toro & Cabezas. The first two genera are reciprocally monophyletic, and together they comprise the sister group of the last two which are also reciprocally monophyletic. *Colletes* has a nearly cosmopolitan distribution but is particularly diverse in semiarid to arid regions of the world, such as the American southwest and central Asia where the genus has been widely studied. On the other hand, the South American fauna of *Colletes* has historically received little attention—despite its richness and uniqueness—by bee taxonomists. As a result, a large proportion of the species found in the continent remain undescribed and most of those that are known to science cannot be unequivocally identified. In the light of this scenario, the second major objective of this dissertation is to revise as much of the South American species of *Colletes* as possible. This objective is tackled in two parts: I firstly revised the species of the genus found in Chile (31 species), and then I revised those distributed in Brazil, Paraguay and Uruguay (19 species). Finally, a comprehensive dated phylogeny of *Colletes* is provided based on Bayesian analyses of DNA sequence data of six different loci. This approach allowed for the accomplishment of the last two major objectives of this dissertation, namely, to propose an intrageneric classification for the *Colletes* of the world, and to reconstruct its historical biogeography in the light of geological and palaeoenvironmental data. The phylogenetic analyses provide strong support for the monophyly of *Colletes* and show that its tree of life consists of five major lineages. The biogeographic reconstructions suggest that *Colletes* originated within the Neotropics in the early Oligocene (*c.* 33 Mya), and that its extant lineages began diversifying only in the later Oligocene (*c.* 27 Mya). They also infer that by the end of the Oligocene *Colletes* had already colonized both the Northern Hemisphere and the Old World which shows a remarkable power of geodispersal.



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## Statement of Authorship

I, Rafael Ferrari, declare for all purposes that the present Ph.D. dissertation entitled “Systematics and biogeography of Colletinae with revisionary studies of the species of *Colletes* Latreille (Hymenoptera: Colletidae: Colletinae) from Chile and eastern South America” was entirely written by me. I am the sole author of Chapters 1, 3 and 4 even though I have been provided with intellectual support by my advisor, Professor Laurence Packer, throughout the preparation of these manuscripts. I am also the primary author of Chapters 2 and 5, however, both were elaborated in collaboration with other researchers, whose contributions were as follows. Chapter 2, which is a morphology-based evolutionary study of the bee subfamily Colletinae, is co-authored by LP who initially obtained most of the examined material via loans from some of the most important bee collections in the world, and later carefully checked the entire dataset matrix that I had assembled through examination of the bee specimens under a stereomicroscope. Chapter 5, which is a molecular evolutionary study of the megadiverse and widespread bee genus *Colletes*, is the result of an extensive collaborative work between me, LP and two laboratory mates – Dr. Thomas Onuferko and M.Sc. Spencer Monckton. The four of us contributed with especially preserved specimens collected in the field. Molecular work (*i.e.* DNA extraction and amplification) was shared among me, TO and SM. TO and SM provided invaluable assistance with the phylogenetic and biogeographic methods, respectively. Therefore, co-authorship in all cases seem justifiable.

Lastly, I also state that 1) the ideas of both Chapters 2 and 5 were originally conceived by me and then further improved by LP; 2) all analyses conducted for the purpose of the two chapters were conducted solely by me; and 3) the aforementioned collaborators, who consent to being co-authors in the corresponding chapters, provided constructive criticisms on the various manuscript drafts written by me.

## Table of Contents

Abstract .....	ii
Acknowledgements .....	iii
Statement of Authorship .....	iv
Table of Contents .....	v
List of Tables .....	vii
List of Figures .....	viii
Chapter 1: Introduction .....	1
Glossary .....	3
References .....	5
Chapter 2: Morphological phylogeny and generic classification of Colletinae (Hymenoptera: Colletidae) .....	10
Abstract .....	10
Introduction .....	11
Material and methods .....	17
Results .....	21
Discussion .....	62
Acknowledgements .....	70
References .....	70
Appendix I: Supplementary tables .....	79
Appendix II: Supplementary figures .....	96
Chapter 3: Taxonomic revision of the species of <i>Colletes</i> Latreille, 1802 (Hymenoptera: Colletidae: Colletinae) found in Chile .....	98
Abstract .....	98
Introduction .....	99
Materials and Methods .....	100
Results .....	105
Key to the Chilean species of <i>Colletes</i> .....	289
Acknowledgements .....	307

References.....	308
Appendix I: Supplementary tables.....	320
Chapter 4: A revision of <i>Colletes</i> Latreille (Hymenoptera: Colletidae: Colletinae) from Brazil, Paraguay and Uruguay.....	327
Abstract.....	327
Introduction.....	328
Materials and Methods.....	329
Taxonomy.....	333
Key to the <i>Colletes</i> species found in Brazil, Paraguay and Uruguay.....	455
Discussion.....	466
Acknowledgements.....	467
References.....	468
Appendix I: Supplementary tables.....	482
Chapter 5: The evolutionary history of <i>Colletes</i> Latreille (Hymenoptera: Colletidae): molecular phylogeny, biogeography and implications for a global intrageneric classification.....	484
Abstract.....	484
Introduction.....	485
Material and methods.....	487
Results.....	495
Discussion.....	501
Conclusion.....	516
Acknowledgements.....	517
References.....	518
Appendix I: Supplementary tables.....	542
Appendix II: Supplementary figures.....	567

## List of Tables

### Chapter 2

Table S1. Alternative generic classifications of Colletinae currently available .....	79
Table S2. List of the species included in the analyses of this study .....	80
Table S3. Discrete character matrix .....	82
Table S4. Continuous character matrix .....	94

### Chapter 3

Table S1. List of the barcoded <i>Colletes</i> specimens .....	320
Table S2. List of the <i>Colletes</i> species and the floral associations .....	325

### Chapter 4

Table S1. Information of the barcoded specimens of each <i>Colletes</i> species .....	482
Table S2. List of the <i>Colletes</i> species and their floral hosts .....	483

### Chapter 5

Table S1. List of the species sampled and GenBank accession numbers .....	542
Table S2. List of the studied specimens .....	547
Table S3. List of the species for which DNA barcodes were obtained .....	550
Table S4. Sequences of the primers used in the PCR amplifications .....	553
Table S5. Species groups of <i>Colletes</i> in the Neotropics .....	554
Table S6. Comparison between the available intrageneric classifications of <i>Colletes</i> ...	562

## List of Figures

### Chapter 2

Figure 1. Lateral habitus of some Colletinae showing some of their diversity .....	12
Figure 2. Diagnostic features of Colletinae .....	14
Figure 3. Diagnostic features of Colletinae .....	15
Figure 4. Diagnostic features of Colletinae .....	16
Figure 5. Illustrations of states of characters 1–3 .....	22
Figure 6. Illustrations of states of characters 5–9 .....	23
Figure 7. Illustrations of states of characters 10, 11 and 13 .....	25
Figure 8. Illustrations of states of characters 12, 14–18 and 56 .....	26
Figure 9. Illustrations of states of characters 19 and 20 .....	27
Figure 10. Illustrations of states of characters 22 and 23 .....	28
Figure 11. Illustrations of states of characters 24–27 .....	29
Figure 12. Illustrations of states of characters 28–30, 32, 97 and 102 .....	31
Figure 13. Illustrations of states of characters 33–35 .....	32
Figure 14. Illustrations of states of characters 37, 39, 40 .....	33
Figure 15. Illustrations of states of characters 37 and 38 .....	34
Figure 16. Illustrations of states of characters 41 and 42 .....	35
Figure 17. Illustrations of states of characters 43–53 .....	36
Figure 18. Illustrations of states of characters 57–60 .....	37
Figure 19. Illustrations of states of characters 68–71 .....	38
Figure 20. Illustrations of states of characters 63–65 and 67 .....	39
Figure 21. Illustrations of states of characters 72, 77 and 79 .....	41
Figure 22. Illustrations of states of characters 80–82 .....	42
Figure 23. Illustrations of states of character 84 .....	43
Figure 24. Illustrations of states of characters 85–87 .....	44
Figure 25. Illustrations of states of characters 98, 99, 101 and 103–105 .....	46
Figure 26. Illustrations of states of characters 106, 110 and 115–119 .....	47
Figure 27. Illustrations of states of characters 121 and 123–129 .....	49
Figure 28. Illustrations of states of characters 130–135 .....	50

Figure 29. Illustrations of states of characters 136–138 and 140 .....	51
Figure 30. Illustrations of states of characters 139, 143 and 149 .....	52
Figure 31. Illustrations of states of characters 144–146 .....	53
Figure 32. Illustrations of states of characters 142, 144–148 .....	54
Figure 33. Indication on how the continuous characters were measured .....	55
Figure 34. Most parsimonious tree from the EW analysis of the combined data .....	57
Figure 35. Fittest tree from the IW analysis of the combined data .....	59
Figure 36. Fittest tree (part 1) with the character state changes mapped on it .....	60
Figure 37. Fittest tree (part 2) with the character state changes mapped on it .....	61
Figure S1. Strict consensus of the 92 most parsimonious trees from the EW analysis of the discrete characters .....	96
Figure S2. Fittest tree from the IW analysis of the discrete characters .....	97

### Chapter 3

Figure 1. Habitus images of both sexes of <i>C. alocochila</i> .....	107
Figure 2. Male terminalia of <i>C. alocochila</i> .....	110
Figure 3. Geographic distribution by <i>Colletes</i> species .....	112
Figure 4. Habitus images of both sexes of <i>C. arthuri</i> .....	115
Figure 5. Male terminalia of <i>C. arthuri</i> .....	117
Figure 6. Habitus images of both sexes of <i>C. atacamensis</i> .....	120
Figure 7. Male terminalia of <i>C. atacamensis</i> .....	123
Figure 8. Habitus images of both sexes of <i>C. atripes</i> .....	126
Figure 9. Male terminalia of <i>C. atripes</i> .....	129
Figure 10. Geographic distribution by <i>Colletes</i> species .....	131
Figure 11. Habitus images of both sexes of <i>C. bicolor</i> .....	134
Figure 12. Male terminalia of <i>C. bicolor</i> .....	137
Figure 13. Habitus images of both sexes of <i>C. chusmiza</i> .....	140
Figure 14. Male terminalia of <i>C. chusmiza</i> .....	144
Figure 15. Habitus images of both sexes of <i>C. cognatus</i> .....	146
Figure 16. Male terminalia of <i>C. cognatus</i> .....	148
Figure 17. Habitus images of both sexes of <i>Colletes coquimbensis</i> .....	151
Figure 18. Male terminalia of <i>C. coquimbensis</i> .....	155

Figure 19. Geographic distribution by <i>Colletes</i> species .....	156
Figure 20. Habitus images of both sexes of <i>C. cyanescens</i> .....	158
Figure 21. Male terminalia of <i>C. cyanescens</i> .....	162
Figure 22. Habitus images of both sexes of <i>C. cyaniventris</i> .....	166
Figure 23. Male terminalia of <i>C. cyaniventris</i> .....	170
Figure 24. Habitus images of both sexes of <i>C. flaminii</i> .....	172
Figure 25. Male terminalia of <i>C. flaminii</i> .....	176
Figure 26. Habitus images of both sexes of <i>C. flavipilosus</i> .....	178
Figure 27. Male terminalia of <i>C. flavipilosus</i> .....	181
Figure 28. Habitus images of both sexes of <i>C. fulvipes</i> .....	183
Figure 29. Male terminalia of <i>C. fulvipes</i> .....	186
Figure 30. Geographic distribution by <i>Colletes</i> species .....	188
Figure 31. Habitus images of both sexes of <i>C. gilvus</i> .....	190
Figure 32. Male terminalia of <i>C. gilvus</i> .....	193
Figure 33. Habitus images of female <i>C. guanta</i> .....	198
Figure 34. Habitus images of both sexes of <i>C. kuhlmanii</i> .....	201
Figure 35. Male terminalia of <i>C. kuhlmanii</i> .....	204
Figure 36. Habitus images of both sexes of <i>C. longiceps</i> .....	208
Figure 37. Male terminalia of <i>C. longiceps</i> .....	212
Figure 38. Habitus images of both sexes of <i>C. lucens</i> .....	214
Figure 39. Male terminalia of <i>C. lucens</i> .....	217
Figure 40. Habitus images of both sexes of <i>C. mastochila</i> .....	219
Figure 41. Male terminalia of <i>C. mastochila</i> .....	222
Figure 42. Habitus images of both sexes of <i>C. murinus</i> .....	226
Figure 43. Male terminalia of <i>C. murinus</i> .....	229
Figure 44. Habitus images of both sexes of <i>C. musculus</i> .....	231
Figure 45. Male terminalia of <i>C. musculus</i> .....	234
Figure 46. Geographic distribution by <i>Colletes</i> species .....	236
Figure 47. Habitus images of both sexes of <i>C. nigrutilus</i> .....	238
Figure 48. Male terminalia of <i>C. nigrutilus</i> .....	241
Figure 49. Habitus images of both sexes of <i>C. nigropilosus</i> .....	244



Figure 50. Male terminalia of <i>C. nigropilosus</i> .....	248
Figure 51. Habitus images of both sexes of <i>C. patagonicus</i> .....	251
Figure 52. Male terminalia of <i>C. patagonicus</i> .....	252
Figure 53. Habitus images of female <i>C. quelu</i> .....	255
Figure 54. Habitus images of both sexes of <i>C. rutilans</i> .....	259
Figure 55. Male terminalia of <i>C. rutilans</i> .....	262
Figure 56. Habitus images of both sexes of <i>C. simulatus</i> .....	266
Figure 57. Male terminalia of <i>C. simulatus</i> .....	268
Figure 58. Habitus images of both sexes of <i>C. sulcatus</i> .....	270
Figure 59. Male terminalia of <i>C. sulcatus</i> .....	274
Figure 60. Habitus images of both sexes of <i>C. toroi</i> .....	276
Figure 61. Male terminalia of <i>C. toroi</i> .....	279
Figure 62. Habitus images of female <i>C. ventricarinatus</i> .....	281
Figure 63. Male terminalia of <i>C. ventricarinatus</i> .....	284
Figure 64. Habitus images of the female <i>C. vicugnensis</i> .....	286
Figure 65. Indication on how the measurements cited in the key were obtained .....	290
Figure 66. Lateral view of mesepisternum of female <i>C. kuhlmanni</i> and <i>C. cyanescens</i> , and dorsal view of metasoma of female <i>C. rutilans</i> , <i>C. lucens</i> , <i>C. ventricarinatus</i> and <i>C. alocochila</i> .....	292
Figure 67. Oblique view of head and latero-ventral view of S6 of female <i>C. murinus</i> and <i>C. ventricarinatus</i> .....	294
Figure 68. Frontal view of labrum and lateral view of propodeum of female <i>C. alocochila</i> and <i>C. mastochila</i> .....	295
Figure 69. Inner view of hind leg of female <i>C. coquimbensis</i> and <i>C. atacamensis</i> , and frontal view of face of female <i>C. toroi</i> and <i>C. longiceps</i> .....	296
Figure 70. Lateral view of mesepisternum of female <i>C. cognatus</i> and <i>C. longiceps</i> , and frontal view of face of female <i>C. kuhlmanni</i> and <i>C. longiceps</i> .....	297
Figure 71. Dorsal view of metasoma of female <i>C. atacamensis</i> , <i>C. flavipilosus</i> and <i>C. sulcatus</i> .....	298
Figure 72. Dorsal view of metasoma of female <i>C. musculus</i> , <i>C. kuhlmanni</i> and <i>C. gilvus</i> .. .....	300

Figure 73. Posterior view of metapostnotum of female <i>C. gilvus</i> and <i>C. simulatus</i> , and frontal view of head of male <i>C. chusmiza</i> and <i>C. fulvipes</i> .....	301
Figure 74. Dorsal view of mesosoma and metasoma of male <i>C. atacamensis</i> and <i>C. flavipilosus</i> .....	303
Figure 75. Frontal view of head of male <i>C. mastochila</i> and <i>C. ventricarinatus</i> , and lateral view of propodeum of male <i>C. gilvus</i> and <i>C. murinus</i> .....	305
Figure 76. Dorsal view of metasoma of male <i>C. kuhlmanni</i> , <i>C. toroi</i> and <i>C. sulcatus</i> .....	307

#### Chapter 4

Figure 1. Lateral view of forewing and posterior view of metapostnotum of female <i>Colletes</i> and <i>Rhynchocolletes</i> .....	335
Figure 2. Habitus images of both sexes <i>C. altimontanus</i> .....	337
Figure 3. Male terminalia of <i>C. altimontanus</i> .....	340
Figure 4. Geographical distribution of <i>C. altimontanus</i> , <i>C. kerri</i> and <i>C. pampeanus</i> .....	342
Figure 5. Habitus images of both sexes <i>C. argentinus</i> .....	344
Figure 6. Male terminalia of <i>C. argentinus</i> .....	347
Figure 7. Geographical distribution of <i>C. argentinus</i> and <i>C. chicoi</i> .....	351
Figure 8. Habitus images of male <i>C. chicoi</i> .....	352
Figure 9. Male terminalia of <i>C. chicoi</i> .....	355
Figure 10. Habitus images of both sexes <i>C. cyaneus</i> .....	358
Figure 11. Male terminalia of <i>C. cyaneus</i> .....	360
Figure 12. Geographical distribution of <i>C. cyaneus</i> , <i>C. flagellaris</i> and <i>C. sertanicola</i> .....	361
Figure 13. Habitus images of female <i>C. ferenudus</i> .....	363
Figure 14. Geographical distribution of <i>C. ferenudus</i> and <i>C. petropolitanus</i> .....	367
Figure 15. Habitus images of both sexes <i>C. flagellaris</i> .....	370
Figure 16. Male terminalia of <i>C. flagellaris</i> .....	372
Figure 17. Habitus images of both sexes <i>C. furfuraceus</i> .....	375
Figure 18. Male terminalia of <i>C. furfuraceus</i> .....	378

Figure 19. Geographical distribution of <i>C. furfuraceus</i> , <i>C. michenerianus</i> and <i>C. rufipes</i> .....	379
Figure 20. Habitus images of both sexes <i>C. hawkingi</i> .....	381
Figure 21. Male terminalia of <i>C. hawkingi</i> .....	385
Figure 22. Geographical distribution of <i>C. hawking</i> and <i>C. meridionalis</i> .....	387
Figure 23. Habitus images of female <i>C. imbricatus</i> .....	388
Figure 24. Geographical distribution of <i>C. imbricatus</i> and <i>C. rugicollis</i> .....	391
Figure 25. Habitus images of both sexes <i>C. kerri</i> .....	393
Figure 26. Male terminalia of <i>C. kerri</i> .....	396
Figure 27. Habitus images of both sexes <i>C. meridionalis</i> .....	399
Figure 28. Male terminalia of <i>C. meridionalis</i> .....	404
Figure 29. Habitus images of both sexes <i>C. michenerianus</i> .....	407
Figure 30. Male terminalia of <i>C. michenerianus</i> .....	410
Figure 31. Habitus images of female <i>C. ornatus</i> .....	414
Figure 32. Male terminalia of <i>C. ornatus</i> .....	415
Figure 33. Geographical distribution of <i>C. ornatus</i> and <i>C. sexangulus</i> .....	417
Figure 34. Habitus images of both sexes <i>C. pampeanus</i> .....	419
Figure 35. Male terminalia of <i>C. pampeanus</i> .....	421
Figure 36. Habitus images of both sexes <i>C. petropolitanus</i> .....	426
Figure 37. Male terminalia of <i>C. petropolitanus</i> .....	428
Figure 38. Habitus images of both sexes <i>C. rufipes</i> .....	433
Figure 39. Male terminalia of <i>C. rufipes</i> .....	438
Figure 40. Habitus images of both sexes <i>C. rugicollis</i> .....	440
Figure 41. Male terminalia of <i>C. rugicollis</i> .....	443
Figure 42. Habitus images of both sexes <i>C. sertanicola</i> .....	448
Figure 43. Male terminalia of <i>C. sertanicola</i> .....	450
Figure 44. Habitus images of female <i>C. sexangulus</i> .....	452
Figure 45. Frontal view of head and dorsal view of mesosoma of female <i>C. cyaneus</i> and <i>C. michenerianus</i> .....	456
Figure 46. Latero-dorsal view of head and dorsal view of metasoma of female <i>C. argentinus</i> and <i>C. petropolitanus</i> .....	457

Figure 47. Lateral and oblique views of head of female <i>C. argentinus</i> and <i>C. rugicollis</i> .....	458
Figure 48. Inner view of hind tibia of female <i>C. altimontanus</i> and <i>C. petropolitanus</i> .....	459
Figure 49. Lateral view of mesosoma of female <i>C. ferenudus</i> and <i>C. rufipes</i> .....	459
Figure 50. Dorsal view of metasoma of female <i>C. ferenudus</i> and <i>C. rufipes</i> .....	460
Figure 51. Ventral view of head of female <i>C. flagellaris</i> , <i>C. rufipes</i> , <i>C. michenerianus</i> and <i>C. cyaneus</i> .....	461
Figure 52. Ventral view of mesosoma of female <i>C. meridionalis</i> and <i>C. rufipes</i> .....	462
Figure 53. Frontal view of head of male <i>C. argentinus</i> and <i>C. rugicollis</i> .....	463
Figure 54. Frontal view of head of male <i>C. altimontanus</i> and <i>C. petropolitanus</i> .....	464
Figure 55. Dorsal view of metasoma of male <i>C. chicoi</i> , <i>C. sertanicola</i> and <i>C.</i> <i>meridionalis</i> .....	465
Figure 56. Lateral view of head of male <i>C. kerri</i> and <i>C. meridionalis</i> .....	466
Figure 57. Dorsal view of metasoma of male <i>C. hawking</i> and <i>C. meridionalis</i> .....	468

## Chapter 5

Figure 1. Bayesian tree obtained through analysis of the multilocus dataset matrix in MrBayes .....	496
Figure 2. Maximum clade credibility tree inferred through Bayesian analysis of the multilocus dataset matrix in BEAST .....	499
Figure 3. Ancestral geographic ranges of nodes inferred by the DEC analysis .....	510
Figure S1. Bayesian tree obtained through analysis of the 28S sequence data .....	567
Figure S2. Bayesian tree obtained through analysis of the COI sequence data .....	568
Figure S3. Bayesian tree obtained through analysis of the EF1a sequence data .....	569
Figure S4. Bayesian tree obtained through analysis of the opsin sequence data .....	570
Figure S5. Bayesian tree obtained through analysis of the pol II sequence data .....	571
Figure S6. Bayesian tree obtained through analysis of the <i>wingless</i> sequence data .....	572
Figure S7. Maximum clade credibility tree inferred through Bayesian analysis of the multilocus dataset matrix in BEAST .....	573
Figure S8. Ancestral geographic ranges of nodes inferred by the DIVALIKE analysis .....	574

## Chapter 1: Introduction

The bees of the subfamily Colletinae (Hymenoptera: Colletidae) are typically mid-sized (8–15mm in length), fast-flying and relatively robust and hairy compared to most of their closest colletid relatives (Michener 1989, 2007). As far as the available data are concerned, all Colletinae species for which nests are known are strictly solitary and build their nests in the soil, except *Colletes rufipes* Smith and *Mourecotelles triciliatus* (Toro & Cabezas) which were reported nesting in previously-established cavities (Garófalo *et al.* 2004; Gazola & Garófalo 2009; Dorado *et al.* 2016), and *M. rubicola* (Benoist) which nests in dead, pithy stems (Benoist 1942). At present, the subfamily includes *c.* 545 valid described species (Ascher & Pickering 2019), the large majority of which (*c.* 520 species) belong to the widespread genus *Colletes* Latreille (Michener 1989, 2007; Kuhlmann *et al.* 2009; Bystriakova *et al.* 2018; Ascher & Pickering 2019). The other 25 species are all confined to the Neotropics (most of them found only south of 23° latitude), yet their genus-level placement is controversial and varies significantly among the available classifications (see Toro & Cabezas 1977, 1978; Michener 1989, 2007; Moure & Urban 2002; Moure *et al.* 2007, 2012; Ascher & Pickering 2019). As recently argued by Vences *et al.* (2013), high degrees of instability may hamper both the significance and communication power of classificatory schemes. Thus, the first major objective of this dissertation is to settle the long-standing controversy regarding the systematics of Colletinae. To accomplish it, I constructed a morphological phylogeny based on maximum parsimony analyses of 161 characters from 61 taxa. This study, which is presented as Chapter 2, provides a solid framework for an updated genus-level classification for the subfamily.

The other three major chapters of this dissertation focus on the bees of *Colletes* which, in addition to their impressive diversity, stand out as important elements of the bee fauna for multiple other reasons. First, they are remarkably widespread and can be found on all continents that have bees except Oceania (Michener 1989, 2007; Kuhlmann *et al.* 2009; Ascher & Pickering 2019). Second, *Colletes* are the only known hosts of the widespread cuckoo bees of the genus *Epeolus* Latreille (Hymenoptera: Apidae). This means that *Epeolus* can only reproduce if the females successfully invade nests of particular *Colletes* species to lay her eggs on the food stores previously provisioned by the host bees (Michener 2007; Onuferko 2018). Also, *Colletes* is an important pollinator of a series of plant species of commercial value such as the common ground

cherry (*Physalis longifolia* Nutt.) (Lamke 2019). In spite of their relevance, a significant proportion of the *Colletes* species cannot be unequivocally identified because their original descriptions are insufficiently detailed and/or because no taxonomic keys are available. This problem is even more worrisome when it comes to the South American fauna of the genus which has been the subject of no comprehensive study to date (Michener 1989, 2007), unlike the Eurasian (Noskiewicz 1936), North American (Stephen 1954) and African (Kuhlmann 2007) faunas. In the light of this scenario, the second major objective of this dissertation is to revise as much of the South American species of *Colletes* as possible. This was accomplished through an integrative approach to taxonomy in which morphological, DNA and geographical data were combined to delineate the species (see also Gibbs 2011; Rocha-Filho & Packer 2015; Monckton 2016; Onuferko 2018). The taxonomic component of my dissertation was tackled in Chapters 3 and 4; in the former I revise the *Colletes* species with known geographical distribution in Chile (Ferrari 2017), while in the latter I revise those found in Brazil, Paraguay and/or Uruguay (Ferrari 2019). Together, these four countries cover an area of *c.* 7,850,000 km<sup>2</sup> (corresponding to 55% of the entire South American territory) which is inhabited by 50 of the 75 *Colletes* species found in the continent (Moure *et al.* 2007, 2012), including 16 species new to science. Of particular relevance are the two fully-illustrated taxonomic keys (one per chapter) for all recognized species for each area, provided to facilitate their identification.

Resolving much of the taxonomic impediment associated with the South American species of *Colletes* has offered an encouraging opportunity to attempt understanding the largely unknown relationships among them. The fact that the intrageneric classifications of *Colletes* available at present covers almost exclusively its Old World fauna (Noskiewicz 1936; Warncke 1978; Kuhlmann *et al.* 2009) has made it important that a more comprehensive classification was proposed. Thanks to a series of collecting expeditions conducted in both North and South Americas, I was able to collect, and then extract DNA of, specimens of 56 different species of *Colletes*. The DNA sequences generated from this material, in combination with previously-available sequences from Old World species (see Kuhlmann *et al.* 2009), allowed me to construct a time-calibrated, molecular phylogeny of *Colletes* at a global scale. Phylogenetic analyses were estimated in a Bayesian framework through which the impact different sources of data (*e.g.* nuclear vs. mitochondrial genes) and different models of DNA evolution (*e.g.* more vs. less parametrized models) were widely explored. Based on the favored phylogenetic tree, I

propose a global intrageneric classification for *Colletes* for the first time thus accomplishing the third major objective of my dissertation. This classification along with the other findings of my molecular phylogenetic study on *Colletes* are presented in Chapter 5.

With a dated phylogeny constructed for *Colletes*, it became possible to analyze its diversification in a historical biogeographic context. Understanding how the major lineages of *Colletes* have achieved their current distribution in the light of geological and palaeoenvironmental data is the fourth and last major objective of this dissertation. While it appears likely that *Colletes* originated within South America (Michener 1979, 1989, 2007; Kuhlmann *et al.* 2009; Almeida *et al.* 2012), the biotic and abiotic factors that may have played an important role in the early stages of its diversification remain unknown. Also, the most important geodispersal events in the biogeographic history of the genus out of South America—*i.e.* towards the Northern Hemisphere and Old World—have never been dated. The historical biogeography of *Colletes* was investigated in a maximum likelihood framework in which ancestral geographical ranges were estimated for its internal nodes. My biogeographic study of *Colletes* is also presented in Chapter 5.

## Glossary

Burn-in phase: number of initial iterations which are discarded and not used to describe the posterior distribution of parameters (Raso *et al.* 2006).

Common ancestor heights: mean age of the most recent common ancestor across the entire set of trees in the posterior distribution (Drummond *et al.* 2012).

Consistency index: measure of the amount of homoplasy implied by the tree. It is calculated as the minimum number of changes in a character matrix divided by the number of changes observed in the tree (Kluge & Farris 1969).

Crown group: monophyletic group that includes the most recent common ancestor of all living species of a more inclusive group plus all daughter species of that ancestor (Martin & Benton 2008).

Geodispersal: expansion of the range of a species in response to the removal of a geographical barrier (Upchurch 2008), as opposed to mere movement of only a short distance made by individuals away from a natal site

Historical biogeography: study of the evolutionary and geological processes that occur over large temporal and spatial scales, which aims to provide hypotheses for explaining discontinuous patterns of distribution of taxa (Santini & Winterbottom 2002).

Homoplasy: condition evolved in two or more taxa as a result of independent evolution (Hall 2007).

Lognormal distribution: distribution of a random variable whose logarithm is normally distributed (Toulias & Kitsos 2013).

Maximum clade credibility tree: tree with the highest product of the posterior probability of all its nodes (Drummond *et al.* 2015).

Neotropics: biogeographic realm consisting of South and Central Americas, Antilles and tropical Mexico (Olson *et al.* 2001).

Operational taxonomic unit: definition of a species or group of species often used in the light of DNA sequence data (Dudhagara *et al.* 2015).

Posterior probability: probability of an event occurring after empirical data has been considered (Liu *et al.* 2004).

Relaxed clock model: model that allows the clock rate to vary among branches of the phylogenetic tree (Boskova *et al.* 2018).

Retention index: measure of how well synapomorphies explain the tree. It is calculated as the maximum number of changes on a tree minus the number of changes on the tree divided by the maximum number of changes on the tree minus the minimum number of changes in the character matrix (Farris 1989).

Synapomorphy: condition evolved in the common ancestor of two or more taxa that is not shared with other taxa (Andreasen 2004).

Stem group: paraphyletic group including all extinct species that diverged earlier than the most recent common ancestor of all living species (Wikstrom *et al.* 2004).

Strict consensus: consensus that includes only the clades consistently repeated in all cladograms being compared (Bremer 1990).



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## Chapter 2: Morphological phylogeny and generic classification of Colletinae (Hymenoptera: Colletidae)

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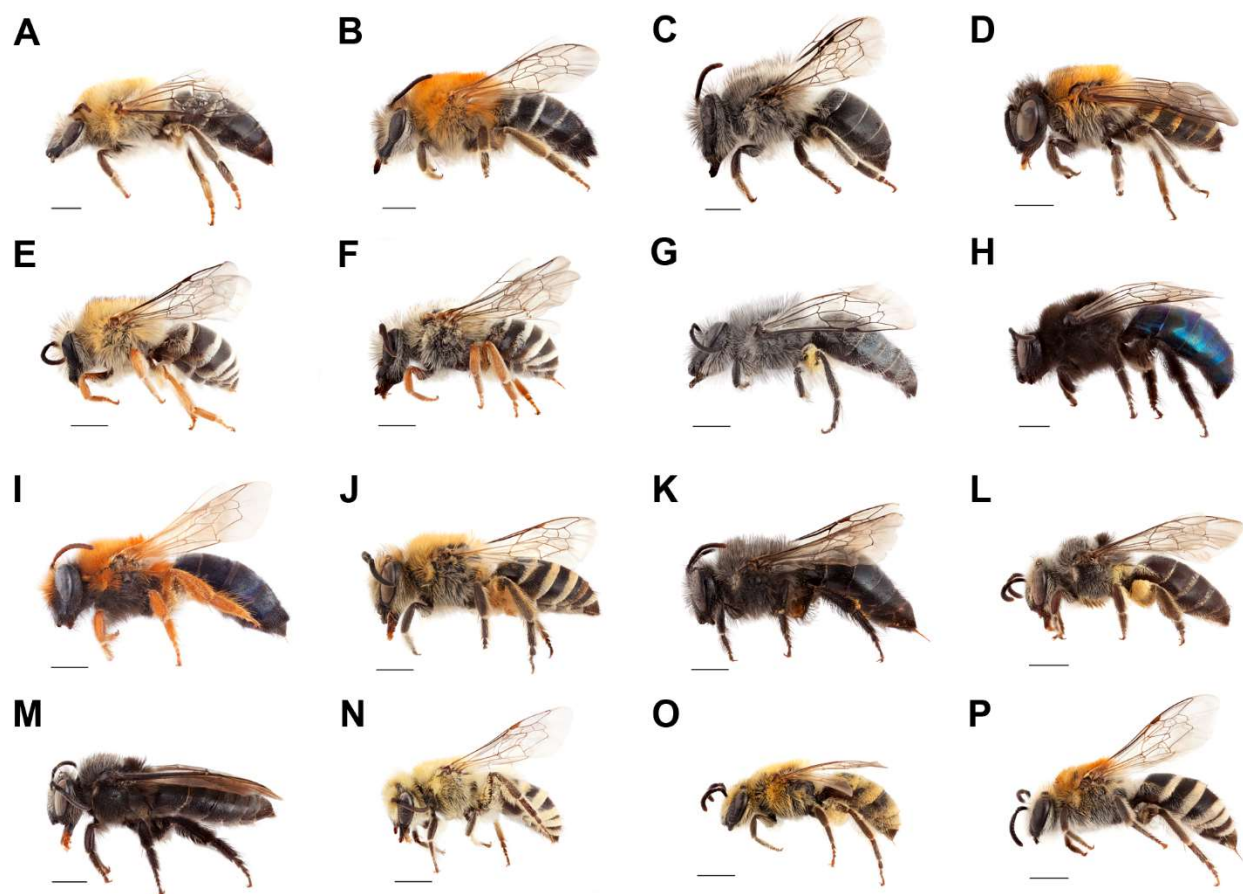
### Abstract

The bee subfamily Colletinae (Hymenoptera: Colletidae) contains roughly 545 valid species, the vast majority of which (*c.* 520) belong to the widespread genus *Colletes* Latreille. The generic placement of the remaining 25 species—which are all confined to the neotropics—has been the subject of a long-standing controversy resulting in several alternative classifications being proposed (the number of accepted genera varies between two to six). The present study provides a morphological phylogeny of the Colletinae constructed through maximum parsimony analyses of 161 characters (149 discrete and 12 continuous). A total of 50 ingroup species were included representing all major lineages of *Colletes* (29 spp.) plus all but five of the non-*Colletes* species of Colletinae (21 spp.). We also sampled a diverse array of outgroups (11 spp.) with a diphaglossine used to root the trees. Our results show that Colletinae is monophyletic and consists of two major clades: one of them includes the reciprocally monophyletic *Mourecotelles* Toro & Cabezas and *Xanthocotelles* Toro & Cabezas; the other contains *Colletes* plus *Hemicotelles* Toro & Cabezas which are also reciprocally monophyletic. *Rhynchocolletes albicinctus* Moure (the type and only species of the genus) belongs to an early branch within *Colletes* and consequently renders the latter paraphyletic. Support for the genera is relatively strong, although their internal relationships are weakly supported overall. A list of diagnostic features of, and a fully-illustrated key for, the recognized genera of Colletinae are provided.

## Introduction

The classification of Colletinae, one of the eight subfamilies currently recognized in the bee family Colletidae (see Almeida *et al.*, 2012, 2019), has been the subject of a long standing controversy amongst bee systematists. In an early paper on the phylogeny and classification of bees (Michener, 1944), Colletinae was considered in its broadest sense to include Paracolletini s.l. (= *Paracolletes* Smith plus Callomelittinae, Neopasiphaeinae and Scrapperinae of Almeida *et al.* [2012, 2019]) and Caupolicaniini (now classified among the Diphaglossinae; see Michener, 2007). Despite the phylogenetic study by Alexander & Michener (1995) on short-tongued bees which indicated that Colletinae (sensu Michener [1944]) was not monophyletic, the subfamily was later delimited in a conservative way once again (Michener, 2007), including Scrapperini and Paracolletini s.l. (with *Scrapper* Lepeletier de Saint-Fargeau & Serville removed). However, more recent classifications consider Colletinae in a narrower sense in which only the widespread genus *Colletes* Latreille and its closest relatives from South America are included (Ascher & Pickering, 2019). This view follows the results of recently published molecular phylogenies of colletid bees (Almeida & Danforth, 2009; Almeida *et al.*, 2012). As treated herein, Colletinae corresponds to the tribe Colletini of various authors, such as Michener (1944, 1989, 2007), Moure & Urban (2002), Melo & Gonçalves (2005), and Moure *et al.* (2007, 2012).

The Colletinae (Fig. 1) are typically mid-sized bees (rarely shorter than 8mm or larger than 15mm), and relatively robust and hairy compared to most colletids (Michener, 1989). In these aspects, they resemble the smaller members of Diphaglossinae (including *Paracolletes*; see Almeida *et al.*, 2019), many Neopasiphaeinae and some Scrapperinae, but are superficially very different from the small, slender and little hairy representatives of the “wasp-like” subfamilies Callomelittinae, Euryglossinae, Hylaeinae and Xeromelissinae (Michener, 2007). The Colletinae can be distinguished from the other robust, hairy colletids by the following characteristics: (i) glossa weakly bilobed (glossa deeply bifid in the Diphaglossinae and a few Neopasiphaeinae; Figs 2A,B); (ii) hind tibia without basitibial plate (basitibial plate present in the Diphaglossinae, Neopasiphaeinae and *Scrapper*, except that it may be weakly developed in the former; Figs 2C,D); (iii) forewing with three submarginal cells (forewing with only two submarginal cells in *Scrapper* and some Neopasiphaeinae; Figs 3A–D); and (iv) T5 and T6 without prepygidial and pygidial fimbriae, respectively (both fimbriae are present in all other hairy colletids; Figs 3E,F).



**Fig. 1.** Lateral habitus of some Colletinae showing some of their diversity. A-P, Females, *Hemicotelles magallanes* (A), *H. ruizii* (B), *Mourecotelles mixtus* (C), *Mourecotelles* sp. (D), *Xanthocotelles atacama* (E), *X. fritzi* (F), *Colletes cyanescens* (G), *C. cyaniventris* (H), *C. fulvipes* (I), *C. halophilus* (J), *C. nigrutilus* (K), *C. petropolitanus* (L), *C. rugicollis* (M), *C. slevini* (N), *C. solidaginis* (O) and *C. zuluensis* (P). Scale bars = 1 mm.

Moreover, the disc of the S7 is remarkably reduced and the whole sternum is essentially represented by its greatly enlarged apicolateral lobes (Fig. 4F) in males of the Colletinae (Michener 1989, 2007). Whether these features are apomorphic for subfamily, however, remains uninvestigated to date.

Currently, Colletinae contains *c.* 545 valid species, the generic placement of which has also been the subject of debate. Michener (1944) considered all species in *Colletes* without recognizing any of the subgenera that had previously been erected within the genus. Later, the same author also adopted *Mourecotelles* Toro & Cabezas, which was subdivided by him into



subgenera to accommodate *Hemicotelles* Toro & Cabezas and *Xanthocotelles* Toro & Cabezas (Michener, 1989, 2007; see also Ascher & Pickering, 2019). In a competing classification, Colletinae was divided into six genera including *Hemicotelles* and *Xanthocotelles*, and the monotypic *Monidia* Cockerell and *Rhynchocolletes* Moure (Moure & Urban, 2002). In more recent classifications, however, *Monidia* and *Mourecotelles* have been considered as junior synonyms of *Colletes* and *Rhynchocolletes*, respectively, thus resulting in four genera being recognized (Moure *et al.*, 2007, 2012). The fact that various alternative, genus-level classifications have already been proposed for Colletinae (summarized in Table S1) further indicates that a comprehensive phylogeny for the subfamily is badly needed.

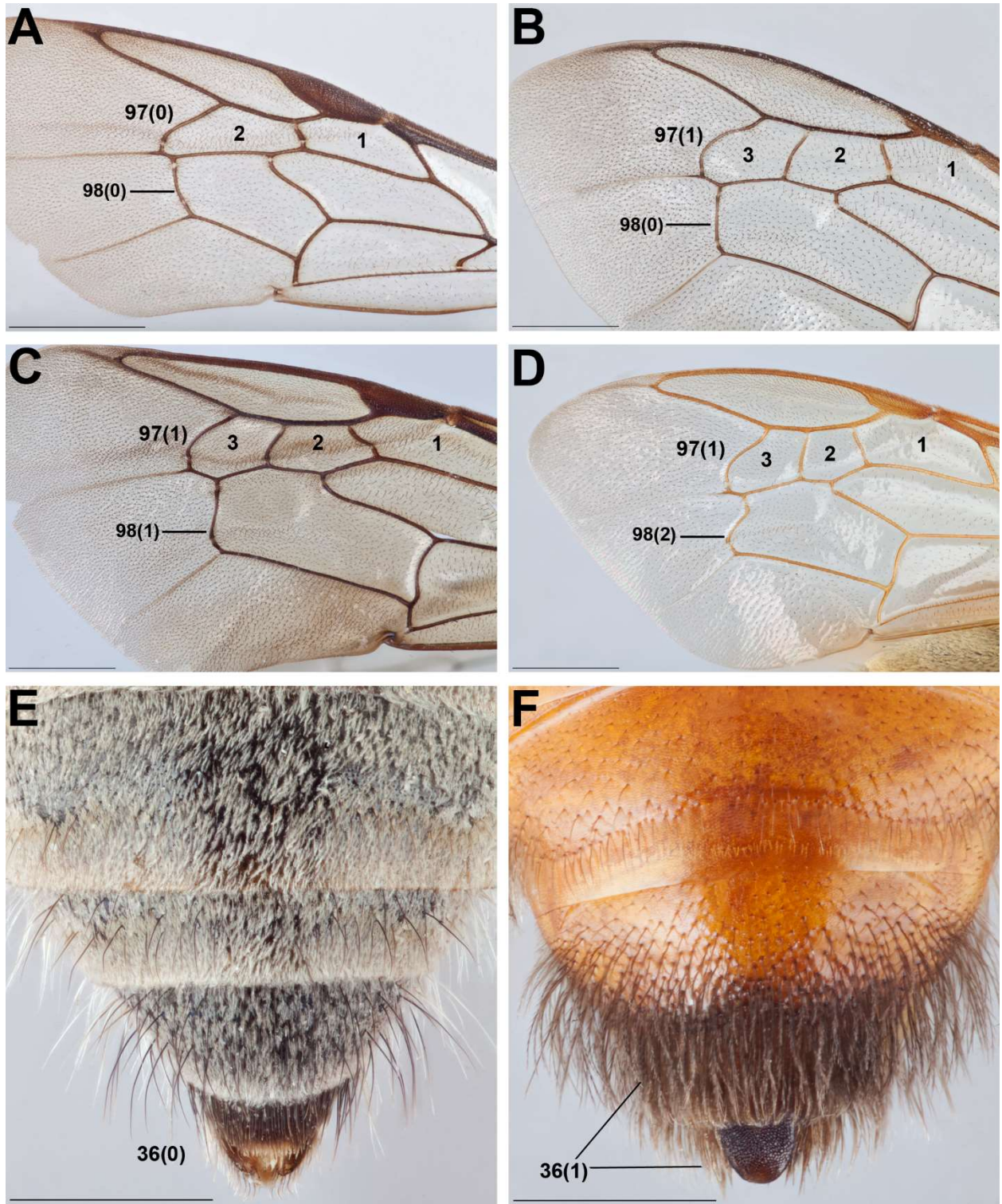
At present, *Colletes* includes *c.* 520 valid species which makes it by far the most speciose genus of Colletinae (Ascher & Pickering, 2019). Although the genus has representatives in all continents (except Oceania), it is particularly rich in the semi-arid regions located at mid-latitudes (Bystriakova *et al.*, 2018). The other genera of Colletinae, however, remain confined to the neotropics (Toro & Cabezas, 1977, 1978; Moure & Urban, 2002; Michener, 2007; Moure *et al.*, 2007, 2012; Ascher & Pickering, 2019). Two characteristics are thought to support the monophyly of *Colletes*, even though they have never been tested in a phylogenetic context: (i) forewing with second recurrent (2m-cu) vein sigmoidal (Fig. 3D); and (ii) metapostnotum with subhorizontal surface limited posteriorly by a transverse carina or sharp change in slope, and divided into pits by longitudinal carinae or sinuous striae (Fig. 4E) (Michener, 1989, 2007; Kuhlmann *et al.*, 2009). *Colletes* is monophyletic according to recent parsimony (Kuhlmann *et al.*, 2009) and Bayesian (Almeida & Danforth, 2009; Almeida *et al.*, 2012) analyses of DNA data. The status of the other genera of Colletinae has not been studied phylogenetically to date, which explains much of the controversy that still surrounds the subfamily's generic classification.

The main objectives of the present study are to construct a phylogeny for the Colletinae through maximum parsimony analyses of morphological data and to propose an updated generic classification for these bees. Additionally, we provide diagnoses and a fully-illustrated key for the genera recognized herein.



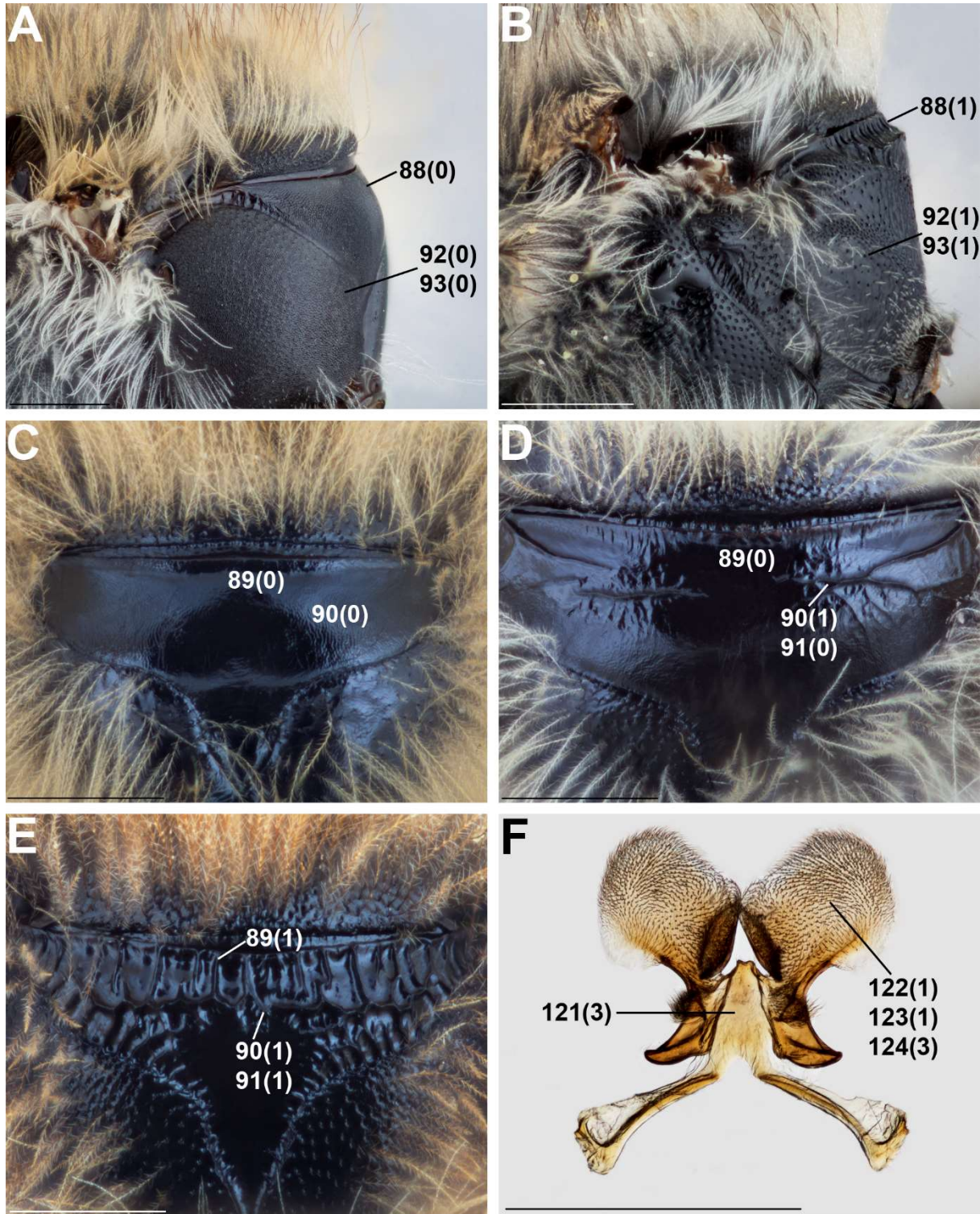
**Fig. 2.** Diagnostic features of Colletinae. A,B, Frontal view of female head showing glossa, *Xanthocotelles atacama* (A) and *Mydrosoma bohartorum* (B); C,D, lateral view of female hind tibia, *Bicolletes rufiventris* (C) and *Colletes gilvus* (D). Scale bars = 1 mm.





**Fig. 3.** Diagnostic features of Colletinae. A-D Lateral view of male forewing, *Hexantheda entrerriana* (A), *Hemicotelles ruizii* (B), *C. albomaculatus* (C) and *C. rufipes* (D); E,F, dorsal view of female metasomal apex, *C. gilvus* (E) and *Bicolletes rufiventris* (F). Scale bars = 1 mm.





**Fig. 4.** Diagnostic features of Colletinae. A,B, Lateral view of male propodeum, *Trichocolletes dowerinensis* (A) and *Colletes gilvus* (B); C-E, posterior view of male metapostnotum, *Xanthocotelles atacama* (C), *Hemicotelles magallanes* (D) and *C. atripes* (E); F, ventral view of male S7 of *Mourecotelles* sp. Scale bars = 1 mm.

## Material and methods

### *Taxon sampling and specimens studied*

The phylogenetic analyses conducted in this study included 61 species-level taxa, 50 Colletinae (ingroup) and 11 outgroups. For the outgroup, we sampled two highly-divergent species of each of the closest relatives of Colletinae—that is, the subfamilies Euryglossinae, Hylaeinae, Neopasiphaeinae, Scrapperinae, and Xeromelissinae—based on previous phylogenetic studies of colletid bees (Magnacca & Danforth, 2006; Packer, 2008; Almeida & Danforth, 2009; Almeida *et al.*, 2012, 2019). *Mydrosoma sabarensis* Silveira & Martines was used to root the trees as the Diphaglossinae are sister to the remaining colletids (Almeida & Danforth, 2009; Almeida *et al.*, 2012). The generic classification of Colletinae initially adopted herein was that of Moure & Urban (2002), in which *Hemicotelles* and *Xanthocotelles* are considered at the generic level and *Rhynchocolletes* is monotypic and valid (Table S1). For the highly diverse genus *Colletes*, we sampled 29 species representing all major clades retrieved by the most comprehensive phylogeny constructed for the genus to date (Kuhlmann *et al.*, 2009), including the various subgenera that were proposed over the 20<sup>th</sup> century (see Michener, 2007: 167) plus the groupings that do not belong to any subgenera available at present: the “African clade”, *C. productus* Robertson group and *C. mixtus* Radoszkowski group (see Kuhlmann *et al.*, 2009). Regarding the sampling of neotropical *Colletes*, for which there has been no proposed intrageneric subdivision, we selected at least one member of each of the various species groups that seem justifiable (see Ferrari & Silveira, 2015; Ferrari, 2017, 2019a, b). With respect to the other genera of Colletinae, we included both described species of *Hemicotelles*, eight of the 12 species of *Mourecotelles* (including one undescribed species from southern Brazil, which is henceforth referred to as *Mourecotelles* sp.), 10 of the 11 species of *Xanthocotelles*, and the single species of *Rhynchocolletes* (*R. albicinctus* Moure). Thus, the only five non-*Colletes* valid species of Colletinae that were unavailable to our analyses were *M. brevipes* (Friese), *M. nigripes* (Friese), *M. rubicola* (Benoist), *M. triciliatus* Toro & Cabezas and *X. plantaris* (Vachal). The type species of all five genera were included. The list of taxa sampled and their locality and repository information are given in Table S2.

We studied material from the following repositories (see Table S2): AMNH – American Museum of Natural History (New York, USA); UFMG – Coleções Taxonômicas da Universidade Federal de Minas Gerais (Belo Horizonte, Brazil); and PCYU – Packer Collection at York University (Toronto, Canada). The New World species of Colletinae were identified by the senior author either through use of available keys (Stephen, 1954; Mitchell, 1960; Toro & Cabezas, 1977, 1978; Ferrari & Silveira, 2015; Balboa *et al.*, 2017; Ferrari, 2017, 2019b) and/or with comparison with primary type specimens. The Old World *Colletes* were identified by Michael Kuhlmann (Kiel University, Germany). The outgroup species were identified by the junior author.

### ***Morphological characters***

The external morphology of adults of both sexes as well as the male terminalia were exhaustively examined under an Olympus SZ61 stereomicroscope with the objective of finding phylogenetically informative characters. Prior to dissection, males were relaxed overnight in plastic containers containing cotton balls soaked in water. The dissected terminalia were cleared with 10% KOH solution and subsequently stored in glycerine within wells of a ceramic plate for easy comparative study. Some of the characters that were coded in our data matrix were originally described and/or illustrated in previous taxonomic studies on the Colletinae (Stephen, 1954; Mitchell, 1960; Toro & Cabezas, 1977, 1978; Michener, 1989; Rojas & Toro, 1993; Toro, 1999; Kuhlmann & Proshchalykin, 2011; Ferrari & Silveira, 2015; Ferrari, 2017, 2019b). The characters that varied similarly between the two sexes were scored solely for males because the females of three species of *Xanthocotelles* (*X. basitarsalis* Toro & Cabezas, *X. subandina* Toro & Cabezas and *X. tarsalis* Toro & Cabezas), as well as that of *R. albicinctus*, were unavailable for study. Nevertheless, the number of female characters in our matrix represented *c.* 35% of the total due to a great number of features exhibited only by females.

Following Sereno (2007), discrete characters were consistently defined as either neomorphic (*i.e.* absent or present) or transformational (*e.g.* rounded or pointed, dark or pale) to avoid inclusion of chimeric characters. This led to contingent coding through which transformational characters were treated as inapplicable for taxa lacking their neomorphic counterparts. To increase the resolution of analyses, we also sampled continuous characters from

body parts the relative size of which has proven to be taxonomically informative for the Colletinae (Stephen, 1954; Mitchell, 1960; Toro & Cabezas, 1977, 1978; Ferrari, 2017). Measurements were taken using a calibrated eyepiece micrometer mounted on a Nikon SMZ1000 stereomicroscope and then converted into ratios to cancel the influence of body length on the obtained measurements. Ratios were calculated from either two different measurements of the same structure (for instance, length and width of the hind basitarsus) or from a single measurement divided by the diameter of the median ocellus (MOD), except head width that was employed as a proxy for body size. Finally, the ratios were rescaled to unity to avoid the influence of different magnitudes on the analyses, as in Koch *et al.* (2015). The continuous characters were analyzed as such (Goloboff *et al.*, 2006), as opposed to being previously discretized (*e.g.* Thiele's [1993] method), a practice that has become common in phylogenetic studies (*e.g.* Hornung-Leoni & Sosa, 2008; Pereyra & Mound, 2010; Álvarez-Padilla & Hormiga, 2011; Lobo *et al.*, 2012; Escapa & Catalanot, 2013), including phylogenies of bees (*e.g.* Monckton, 2016).

The terminology for the external morphology of bees adopted herein is that of Michener (2007), except as follows: (i) the basal and posterior surfaces of the propodeum are referred to as subhorizontal and vertical surfaces of the metapostnotum, respectively (as in Ferrari, 2017); (ii) genal, frontal and vertexal areas are used rather than gena, frons and vertex, respectively (as in Prentice, 1998; Dumesht & Packer, 2013). Terminology for the anatomy of the male terminalia follows Stephen (1954). Integument sculpture and leg surfaces were named in accordance with Harris (1979), except that 'stria' is herein used to define a short, somewhat thick carina rather than impressed sculpture. Terminology for leg surfaces follows Aguiar & Gibson (2010). Antennal flagellomeres and metasomal terga and sterna are referred to with the letters F, T and S, respectively, followed by appropriate numbers. Punctuation density is given in terms of the relative sizes of puncture diameters (d) and the interspaces (i) among them.

### ***Phylogenetic analyses***

The discrete dataset matrix was assembled with Mesquite v.3.51 (Maddison & Maddison, 2008) and subsequently opened in Notepad++ v. 7.5.8 (Notepad-plus-plus.org, 2018) for inclusion of the continuous characters. The resulting file was then exported to TNT v.1.5

(Goloboff *et al.*, 2003a, 2008; Goloboff & Catalano, 2016) where maximum parsimony analyses were conducted.

Phylogenetic trees were estimated through both equal weighting (EW) and extended implied weighting (IW; see Goloboff, 2014) analyses of the combined data. Unlike the original implied weighting (Goloboff, 1993), the extended version of the method can analyze different partitions by assigning them different concavity ( $k$ ) values (Goloboff, 2014). All discrete characters were treated as non-additive, whereas the continuous ones are invariably treated as additive by TNT (Goloboff *et al.*, 2006, 2008). For the IW analysis, we utilized the ‘setk’ script to select optimal values for  $k$ , an approach that has previously been used by authors such as Santos *et al.* (2015) and Monckton (2016). Discrete and continuous characters were analyzed in separate partitions using the  $k$  values determined by setk.

Analyses were conducted using ‘traditional search’, starting with a Wagner tree followed by tree bisection-reconnection (TBR) branch swapping, and saving up to 10 trees per replication. After each analysis, we ran additional rounds of TBR with the trees saved in the memory to maximize the likelihood of finding all most parsimonious trees (or all trees of highest fit). To verify whether the obtained topologies remained stable, the same analysis was repeated with  $10^3$ ,  $10^4$  and  $10^5$  replications. Furthermore, we also performed Ratchet, Drift and Tree fusing from ‘new technology search’ with  $10^3$  replications through ‘driven search’ setting the ‘find minimum length’ to  $10^2$ . Retention and consistency indexes (RI and CI, respectively) were calculated with the ‘stats’ script (available from: <http://tnt.insectmuseum.org/index.php/scripts>).

Support for clades was estimated through symmetric resampling (Goloboff *et al.*, 2003b) and bootstrap (Felsenstein, 1985). The former—which is not influenced by character weights and therefore ideal for measuring support of clades from IW analysis (Goloboff *et al.*, 2003b)—was performed with  $10^3$  replicates with a probability of 33% of character weight change (default value). The supports from symmetric resampling are given as supported/contradicted (GC) values—they represent the difference between the frequency of a particular clade and that of the most frequently recovered, contradictory one. Bootstrap (BS) values were calculated with standard resampling (*i.e.* sampling with replacement) with  $10^3$  replicates, and are given as absolute frequencies.

Winclada v.1.00.08 (Nixon, 2002) was used to edit, and map character state changes onto, the resulting cladograms using unambiguous optimization.



## ***Images***

Most morphological characters were imaged with a Visionary Digital BK Plus Lab System with a Canon EOS 5D Mark II digital camera and Canon Macro MP-E 65mm lens. To image the male terminalia, a Canon Extender EF 2x was connected to the camera to increase its magnification. Multiple images from varying planes of focus were taken with a P-51Cam-Lift high precision Linear Actuator using the software P51 Camlift Controller v.2.6. Then, image slices were imported with Adobe Lighroom v.4.4 and finally exported to Helicon Focus v.5.3.3 where they were amalgamated into a single, multi-focus image. Final images were edited, and mounted into plates, in Adobe Photoshop v.13.0.1.

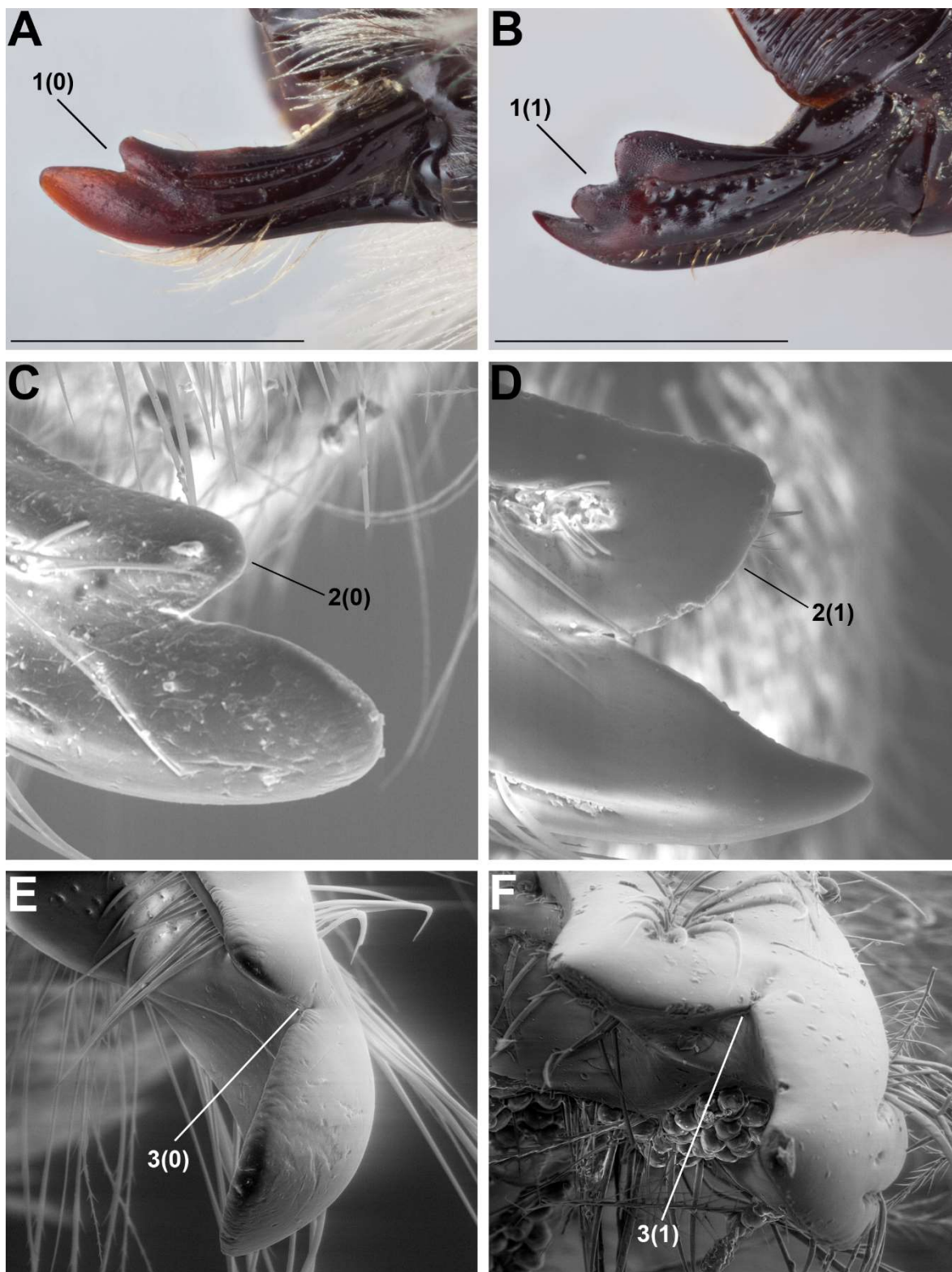
## **Results**

### ***List of characters***

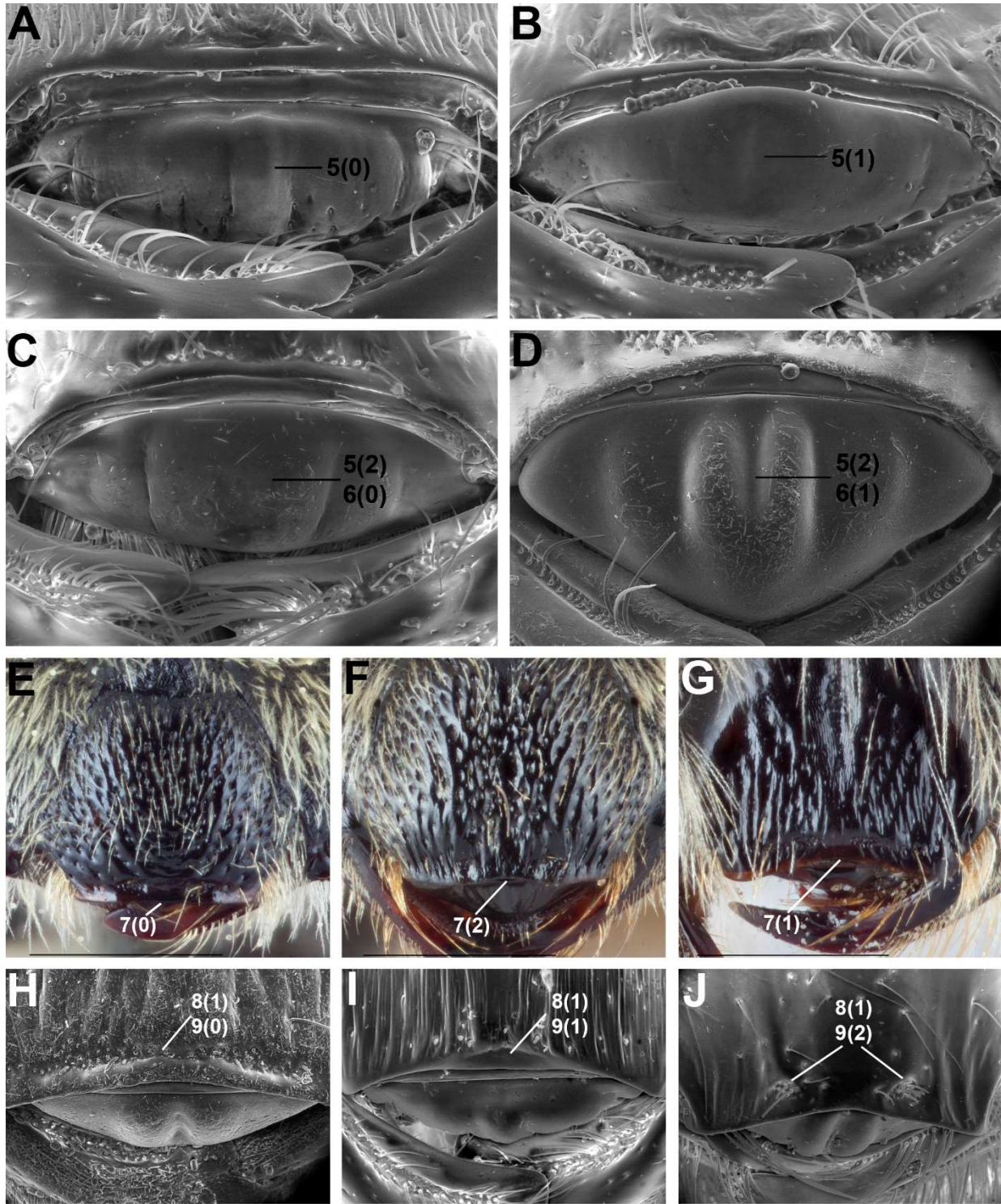
In total, we coded 161 morphological characters of which 149 discrete (1–149) and 12 continuous (150–161). The character list along with their respective states are provided below. The discrete and continuous matrices are in Table S3 and Table S4, respectively. The following  $k$  values were determined by setk and then used in the phylogenetic analyses: discrete characters ( $k = 12.63$ ) and continuous characters ( $k = 4.29$ ).

### ***Female***

1. Mandible, number of preapical teeth: (0) 1 (Fig. 5A); (1) 2 (Fig. 5B).
2. Mandible, shape of lower preapical tooth: (0) narrowly rounded (Fig. 5C); (1) broadly truncate (Fig. 5D).
3. Mandible, angle between apical and preapical teeth: (0) obtuse (Fig. 5E); (1) right (Fig. 5F).
4. Labrum, medial modification: (0) absent; (1) present (Figs 6A–D).
5. Labrum, shape of medial modification: (0) transverse ridge (Fig. 6A); (1) oval depression (Fig. 6B); (2) tubercle (Figs 6C,D). Not applicable for taxa coded as 4(0).



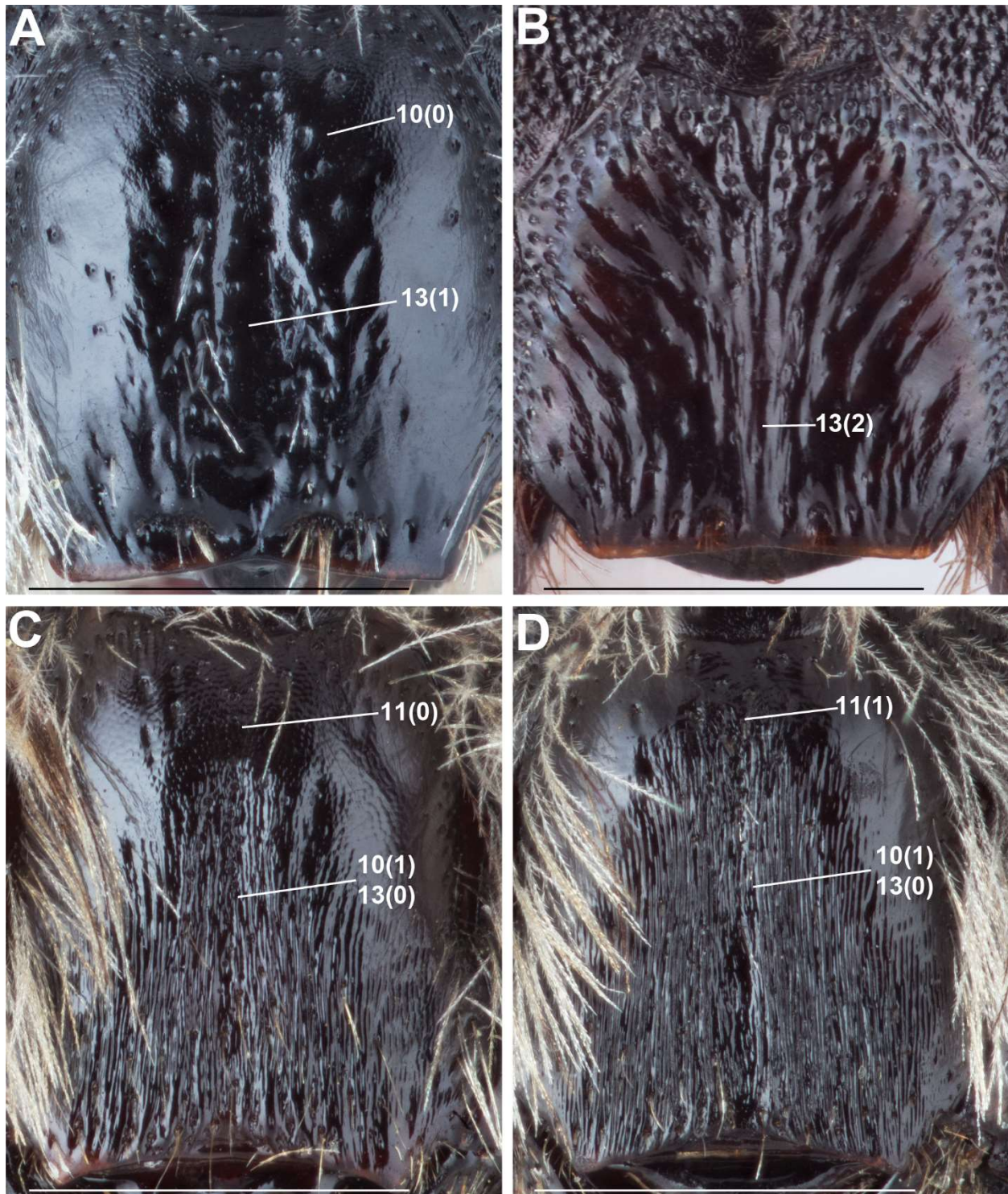
**Fig. 5.** Illustrations of states of characters 1–3. A–D, Outer view of female mandible, *Colletes cyanescens* (A), *Hyleoides concinna* (B), *C. gilvus* (C) and *Mourecotelles mixtus* (D); E, F, inner view of female mandible, *C. gilvus* (E) and *M. mixtus* (F). Scale bars = 1 mm.



**Fig. 6.** Illustrations of states of characters 5–9. A–D, Frontal view of female labrum, *Mourecotelles mixtus* (A), *Colletes clypeonitens* (B), *C. bombiformis* (C) and (D) *C. gilvus*; E–J, frontal view of female clypeus, *C. americanus* (E), *C. petropolitanus* (F), *Hemicotelles ruizii* (G,H), *M. mixtus* (I) and *C. atripes* (J). Scale bars = 1 mm.

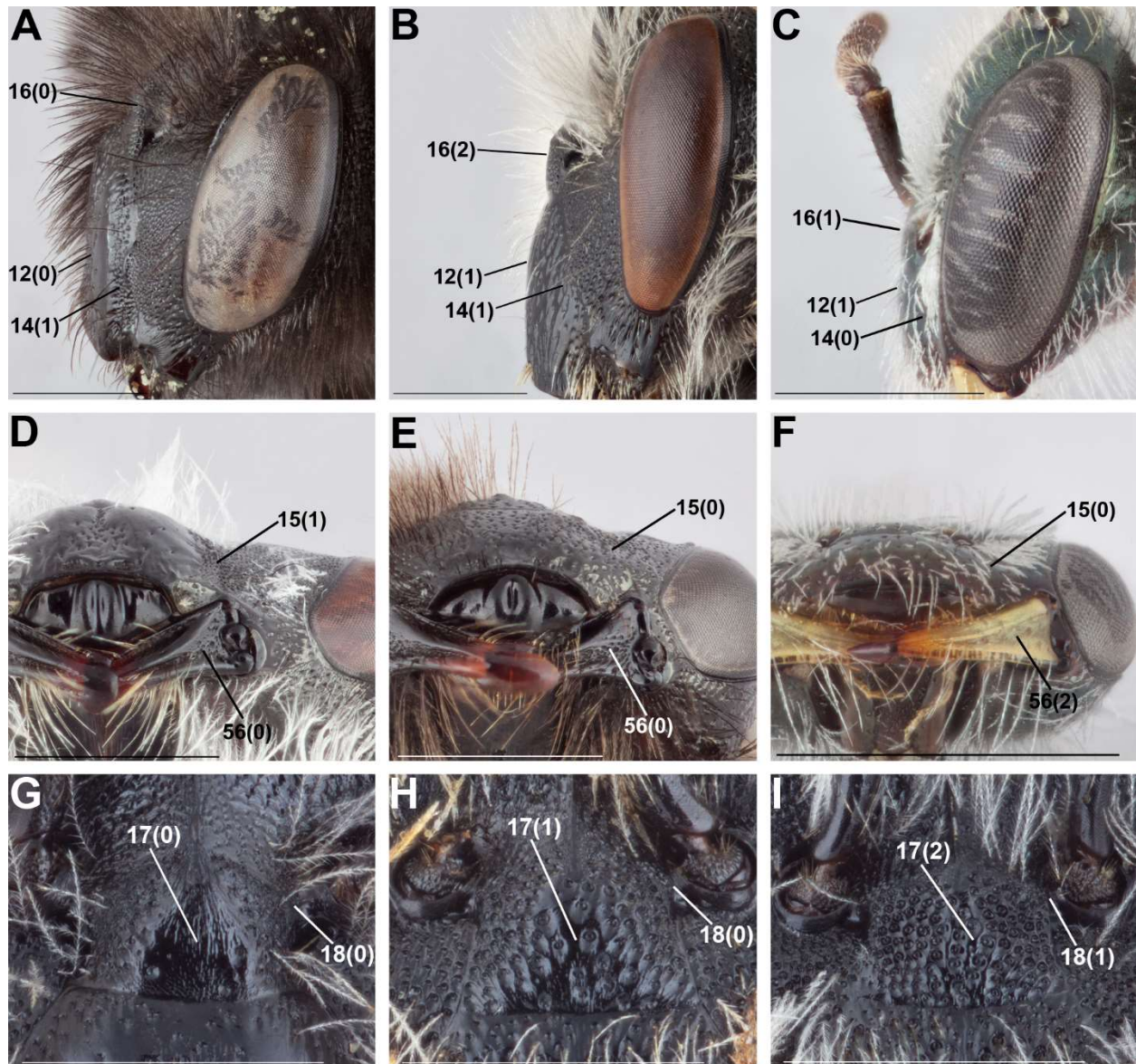


6. Labrum, tubercle, medial longitudinal sulcus: (0) absent (Fig. 6C); (1) present (Fig. 6D). Only applicable for taxa coded as 5(2).
7. Clypeus, shape of lower margin: (0) straight (Fig. 6E); (1) narrowly emarginate (Fig. 6F); (2) broadly concave (Fig. 6G).
8. Clypeus, subapical depression(s): (0) absent; (1) present (Figs 6H–J).
9. Clypeus, shape of subapical depression(s): (0) transverse and long (Fig. 6H); (1) broadly subtriangular (Fig. 6I); (2) pair of subcircular pits (Fig. 6J). Not applicable for taxa coded as 8(0).
10. Clypeus, longitudinal striation: (0) absent (Figs 7A,B); (1) present (Figs 7C,D).
11. Clypeus, relative length of longitudinal striae: (0) relatively short, not reaching upper fourth (Fig. 7C); (1) long, reaching upper fourth (Fig. 7D). Not applicable for taxa coded as 10(0).
12. Clypeus, shape of disc in profile: (0) flat (Fig. 8A); (1) convex (Figs 8B,C).
13. Clypeus, shape of medial longitudinal region: (0) flat (Figs 7C,D); (1) depressed (Fig. 7A); (2) carinate (Fig. 7B).
14. Clypeus, position in relation to paraocular area in profile: (0) same level (Fig. 8C); (1) produced anteriorly (Figs 8A,B).
15. Clypeus, separation from paraocular area in anteroventral view: (0) gradual (Figs 8E,F); (1) abrupt (Fig. 8D). Not applicable for taxa coded as 14(0).
16. Supraclypeal area, position in relation to clypeal upper margin in profile: (0) depressed (Fig. 8A); (1) same level (Fig. 8C); (2) produced anteriorly (Fig. 8B).
17. Supraclypeal area, punctation medially: (0) sparse ( $i > 2d$ ; Fig. 8G); (1) dense ( $i = 0.5–1d$ ; Fig. 8H); (2) very dense ( $i < 0.5d$ ; Fig. 8I).
18. Subantennal suture, intersection with upper margin of supraclypeal area: (0) smoothly curved (Figs 8G,H); (1) angled (Fig. 8I).
19. Frontal line, below: (0) carinate (Fig. 9A); (1) sulcate (Fig. 9B).
20. Facial fovea, appressed short hairs: (0) absent (Fig. 9C); (1) present (Fig. 9D).
21. Vertexal area, shape in posterodorsal view: (0) flat (Ferrari & Silveira, 2015: Fig. 2B); (1) concave (Ferrari & Silveira, 2015: Fig. 2A).
22. Vertexal area, separation from occiput: (0) angulate (Fig. 10A); (1) smoothly curved (Fig. 10B).
23. Genal area, tomentum above: (0) absent (Fig. 10C); (1) present (Fig. 10D).



**Fig. 7.** Illustrations of states of characters 10, 11 and 13. A-D, Frontal view of female clypeus, *Colletes cyanescens* (A), *C. chusmiza* (B), *Mourecotelles chillan* (C) and *M. mixtus* (D). Scale bars = 1 mm.





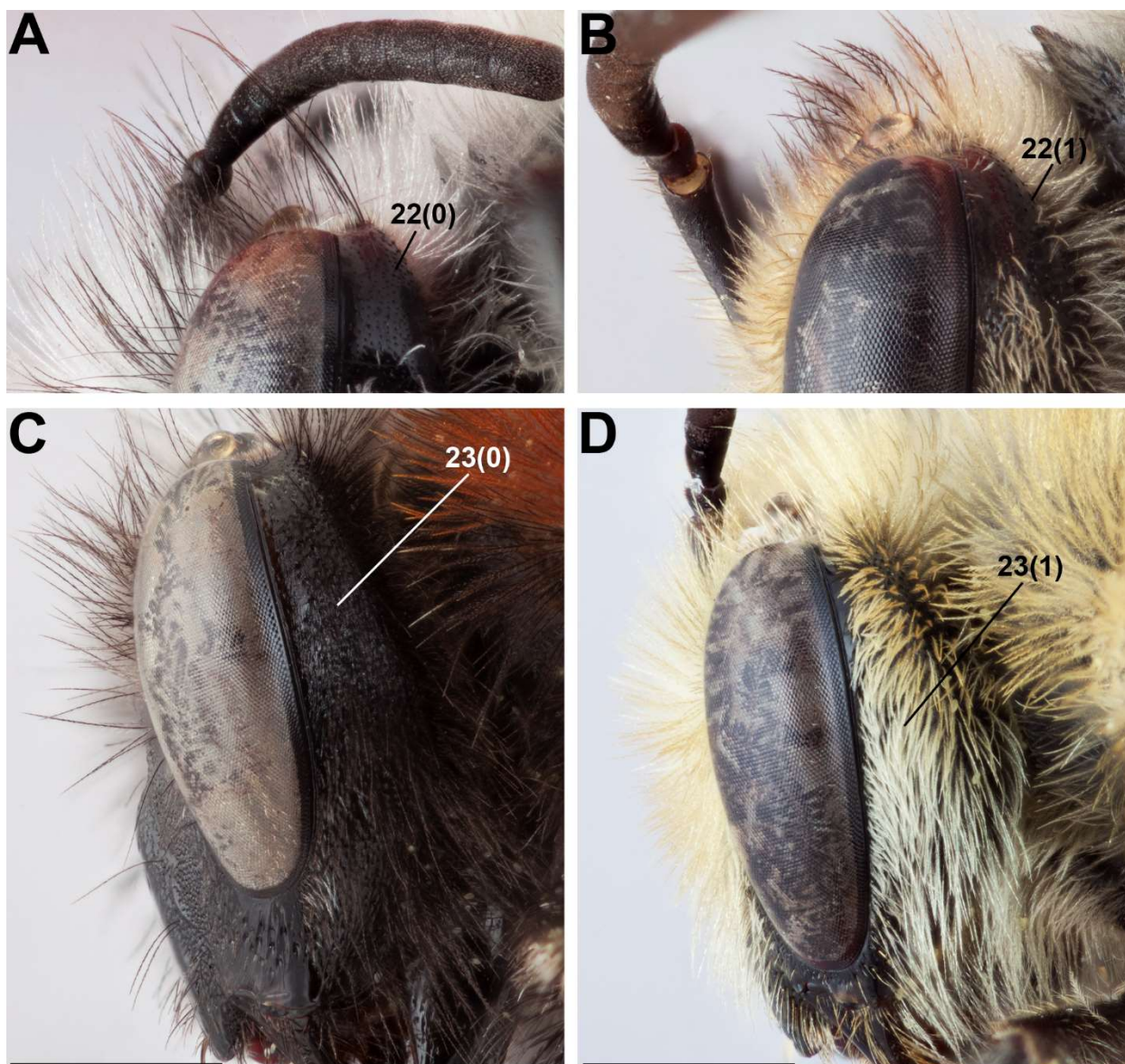
**Fig. 8.** Illustrations of states of characters 12, 14–18 and 56. A–C, Lateral view of female head, *Colletes atripes* (A), *C. coriandri* (B) and *Euhesma sybilae* (C); D–F, anteroventral view of female head, *C. gilvus* (D), *C. petropolitanus* (E) and *E. sybilae* (F); G–I, frontal view of female supraclypeal area, *Mourecotelles mixtus* (G); *C. impunctatus* (H) and *C. eous* (I). Scale bars = 1 mm.





**Fig. 9.** Illustrations of states of characters 19 and 20. A,B, Frontal view of female frontal line, *Colletes fulvopilosus* (A) and *Hylaeus modestus* (B); C,D, oblique view of female facial fovea, *C. gilvus* (C) and *C. rufipes* (D). Scale bars = 1 mm.





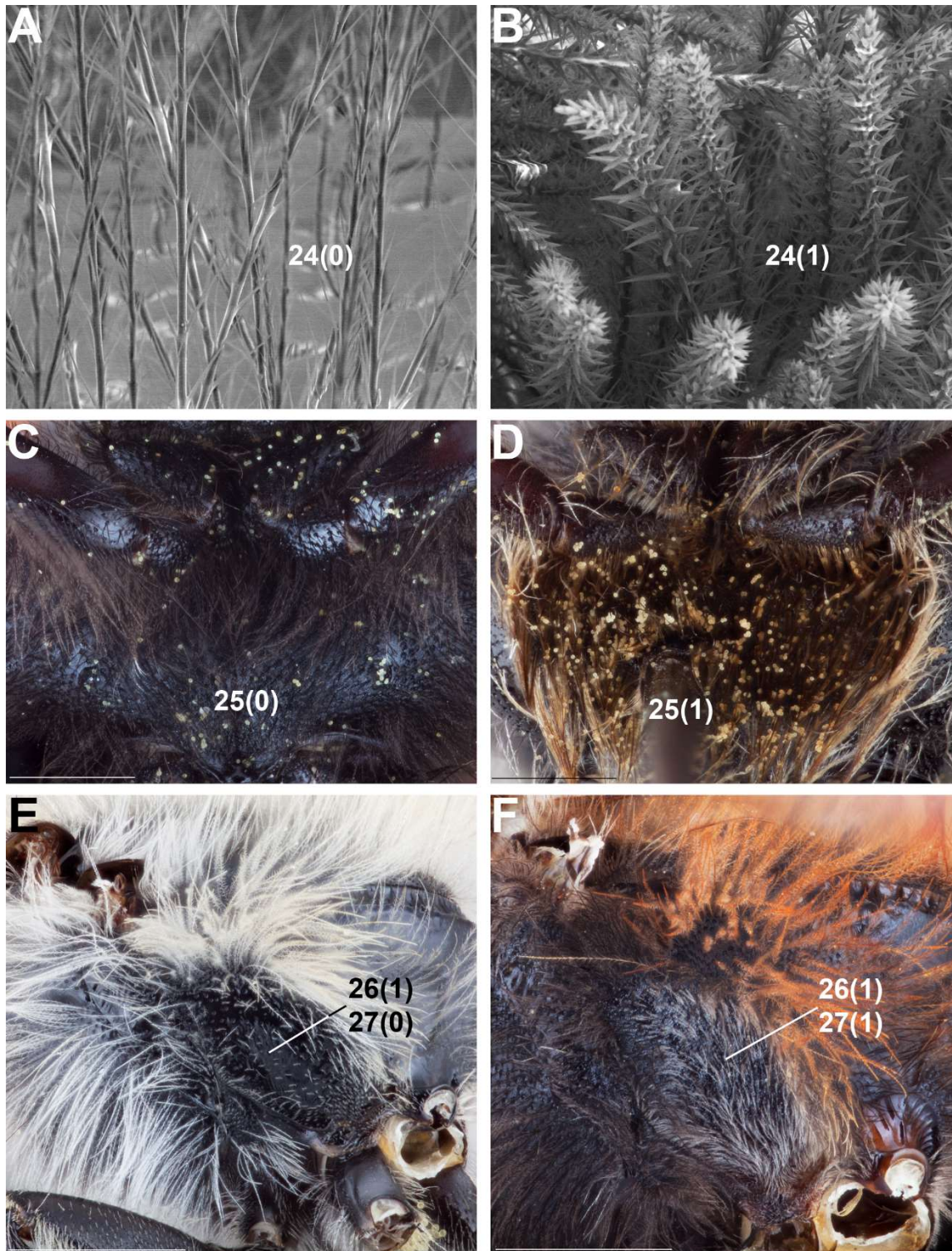
**Fig. 10.** Illustrations of states of characters 22 and 23. A-D, Female head in profile, *Colletes gilvus* (A), *C. petropolitanus* (B), *C. atripes* (C) and *C. eulophi* (D). Scale bars = 1 mm.

**24.** Mesoscutum, branching pattern of hairs: (0) hairs sparsely branched, space between branches evident (Fig. 11A); (1) hairs plumose, space between branches virtually absent (Fig. 11B).

**25.** Mesosoma, density of pubescence ventrally: (0) relatively sparse, integument visible (Fig. 11C); (1) very dense, integument obscured (Fig. 11D).

**26.** Lateral surface of propodeum, tomentose hairs: (0) absent; (1) present (Figs 11E,F).

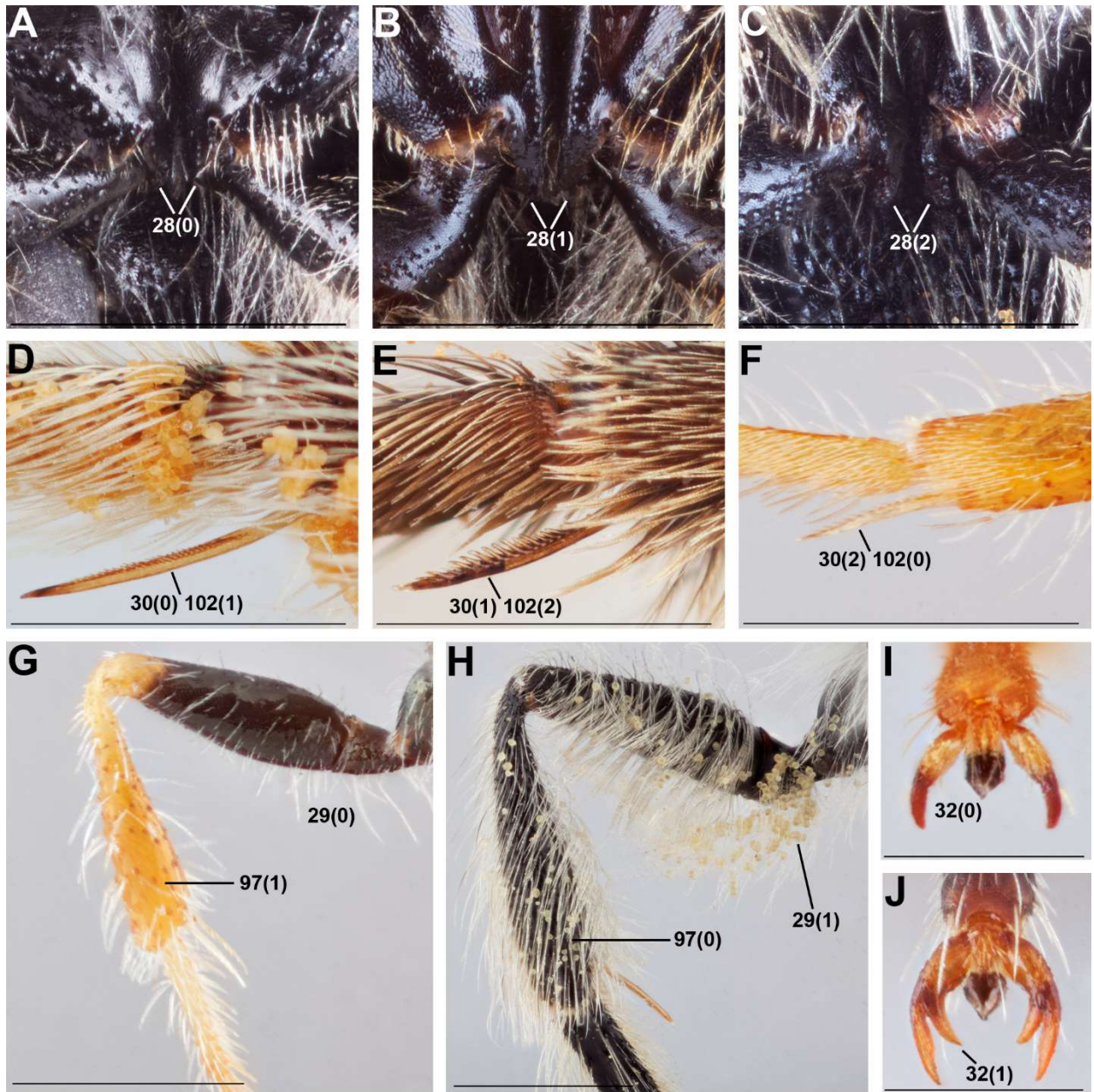




**Fig. 11.** Illustrations of states of characters 24–27. A,B, Scanning electron micrographs of female mesoscutal hairs, *Colletes gilvus* (A) and *C. kozlovi* (B); C,D, ventral view of female mesosoma, *C. atripes* (C) and *C. petropolitanus* (D); E,F, lateral view of female propodeum, *C. gilvus* (E) and *C. atripes* (F). Scale bars = 1 mm.

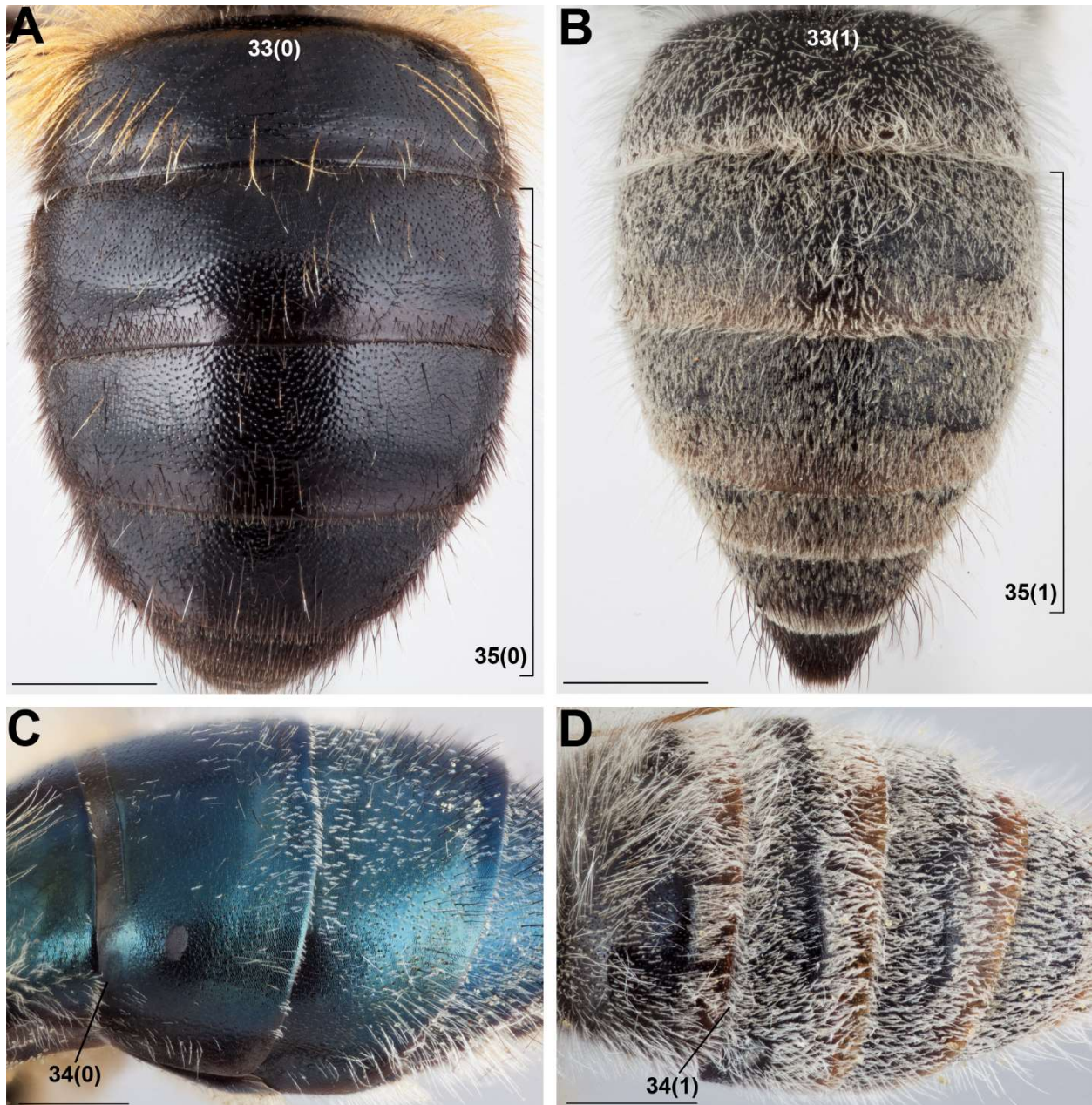
- 27.** Lateral surface of propodeum, density of tomentose hairs: (0) sparse (Fig. 11E); (1) dense (Fig. 11F). Not applicable for taxa coded as 26(0).
- 28.** Front coxa, shape of posteroventral surface: (0) rounded (Fig. 12A); (1) conical (Fig. 12B); (2) a long spine (Fig. 12C).
- 29.** Hind femur, scopa: (0) absent (Fig. 12G); (1) present (Fig. 12H).
- 30.** Hind tibial spur: (0) ciliate (Fig. 12D); (1) pectinate (Fig. 12E); (2) serrate (Fig. 12F).
- 31.** Hind basitarsus, shape of dorsal surface: (0) flat; (1) longitudinally concave.
- 32.** Hind tarsal claws, subapical teeth: (0) absent (Fig. 12I); (1) present (Fig. 12J).
- 33.** T1, disc, tomentum: (0) absent (Fig. 13A); (1) present (Fig. 13B).
- 34.** T2, pregradular area, tomentum: (0) absent (Fig. 13C); (1) present (Fig. 13D).
- 35.** T2–T5, discs, tomentum: (0) absent (Fig. 13A); (1) present (Fig. 13B).
- 36.** T5, prepygidial and pygidial fimbriae: (0) absent (Fig. 3E); (1) present (Fig. 3F).
- 37.** T6, pygidial plate: (0) absent (Figs 14A–C); (1) present (Figs 15A–D).
- 38.** T6, shape of pygidial plate: (0) represented by a broadly rounded plate (Fig. 15A); (1) indicated by a longitudinal ridge (Fig. 15B); (2) indicated by a small tubercle (Fig. 15C); (3) indicated by a strong subtriangular protrusion (Fig. 15D). Not applicable for taxa coded as 37(0).
- 39.** T6, shape of marginal zone in lateral view: (0) not forming a raised lip (Fig. 14D); (1) forming a raised lip (Fig. 14E).
- 40.** T6, shape of marginal zone medially in dorsal view: (0) narrowly rounded (Fig. 14A); (1) broadly rounded (Fig. 14B); (2) broadly truncate (Fig. 14C).
- 41.** S2, pubescence: (0) sparse (Fig. 16A); (1) moderately dense (Fig. 16B); (2) forming a scopa (Fig. 16C).
- 42.** S5, specialized area covered with dense short hairs: (0) absent (Fig. 16D); (1) present (Fig. 16E).
- 43.** S6, relative size: (0) broader than long (Fig. 17A); (1) longer than broad (Figs 17B–F).
- 44.** S6, strong longitudinal ridge laterally: (0) absent (Figs 17A,B,D–F); (1) present (Fig. 17C).
- 45.** S6, weakly sclerotized area: (0) absent (Figs 17A–C); (1) present (Figs 17D–F).
- 46.** S6, location of weakly sclerotized area: (0) medial longitudinal band (Fig. 17D); (1) posteriorly (Fig. 17F); (2) broader midlength narrowing apically (Fig. 17E).
- 47.** S6, yellowish colouration: (0) absent (Figs 17B–F); (1) present (Fig. 17A).



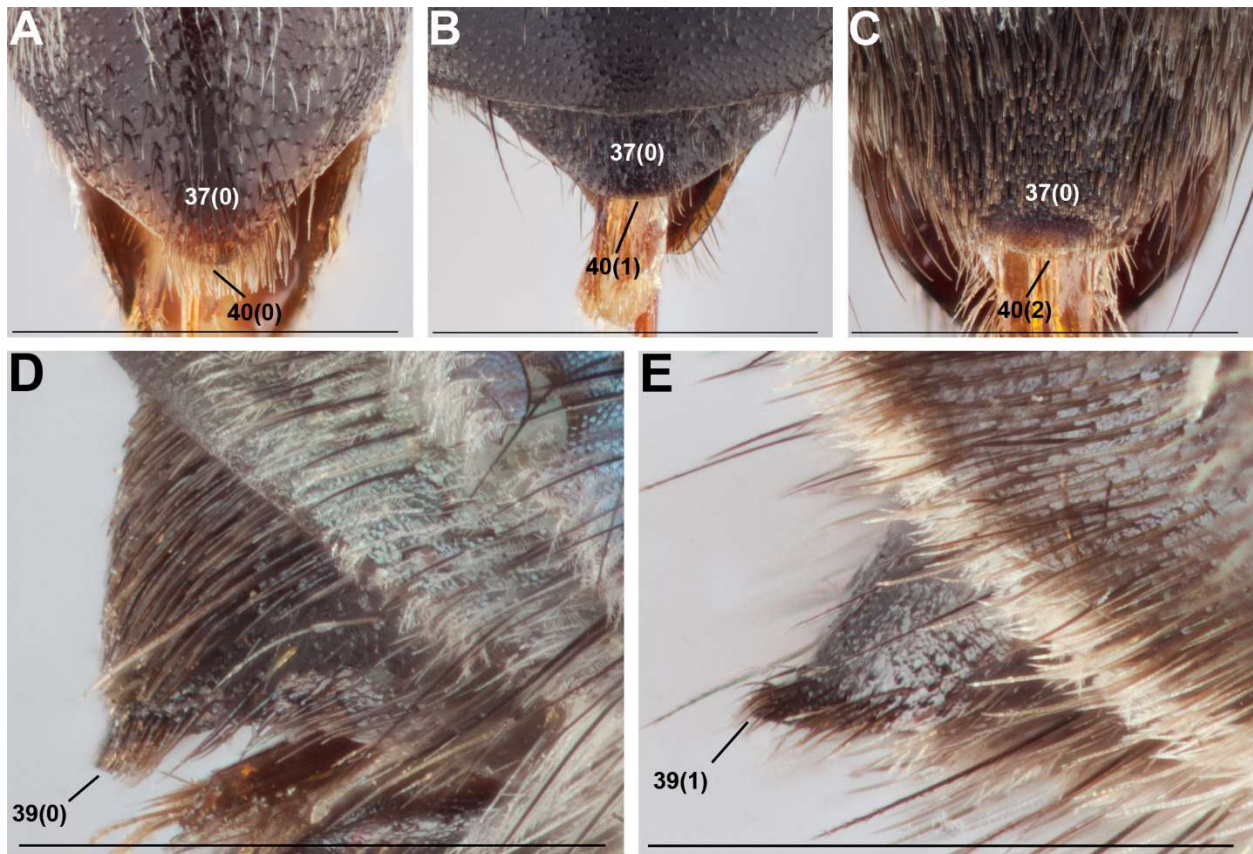


**Fig. 12.** Illustrations of states of characters 28–30, 32, 97 and 102. A–C, Ventral view of female front coxa, *Colletes gilvus* (A), *Xanthocotelles atacama* (B) and *C. americanus* (C); D–F, inner view of female hind tibia showing tibial spur, *C. altimontanus* (D), *C. petropolitanus* (E) and *Euhesma sybilae* (F); G,H, anterior view of female hind leg, *E. sybilae* (G) and *C. gilvus* (H); I,J, dorsal view of female hind tarsal claws, *X. atacama* (I) and *C. gilvus* (J). Scale bars = 1 mm.





**Fig. 13.** Illustrations of states of characters 33–35. A,B, Dorsal view of female metasoma, *Colletes atripes* (A) and *C. gilvus* (B); C,D lateral view of female metasoma, *C. cyanescens* (C) and *C. gilvus* (D). Scale bars = 1 mm.



**Fig. 14.** Illustrations of states of characters 37, 39, 40. A-C, Dorsal view of female T6, *Colletes gilvus* (A), *Mourecotelles mixtus* (B) and *C. cyanescens* (C); D,E, lateral view of T6, *C. cyanescens* (D) and *Mourecotelles* sp. (E). Scale bars = 1 mm.

**48.** S6, size of yellowish marking: (0) small and located posteriorly; (1) throughout (Fig. 17A).

Not applicable for taxa coded as 47(0).

**49.** S6, oblique raised area posterolaterally: (0) absent (Fig. 17G); (1) present (Fig. 17H).

**50.** S6, shape of posterolateral margin: (0) convex (Figs 17A,C–F); (1) straight (Fig. 17B).

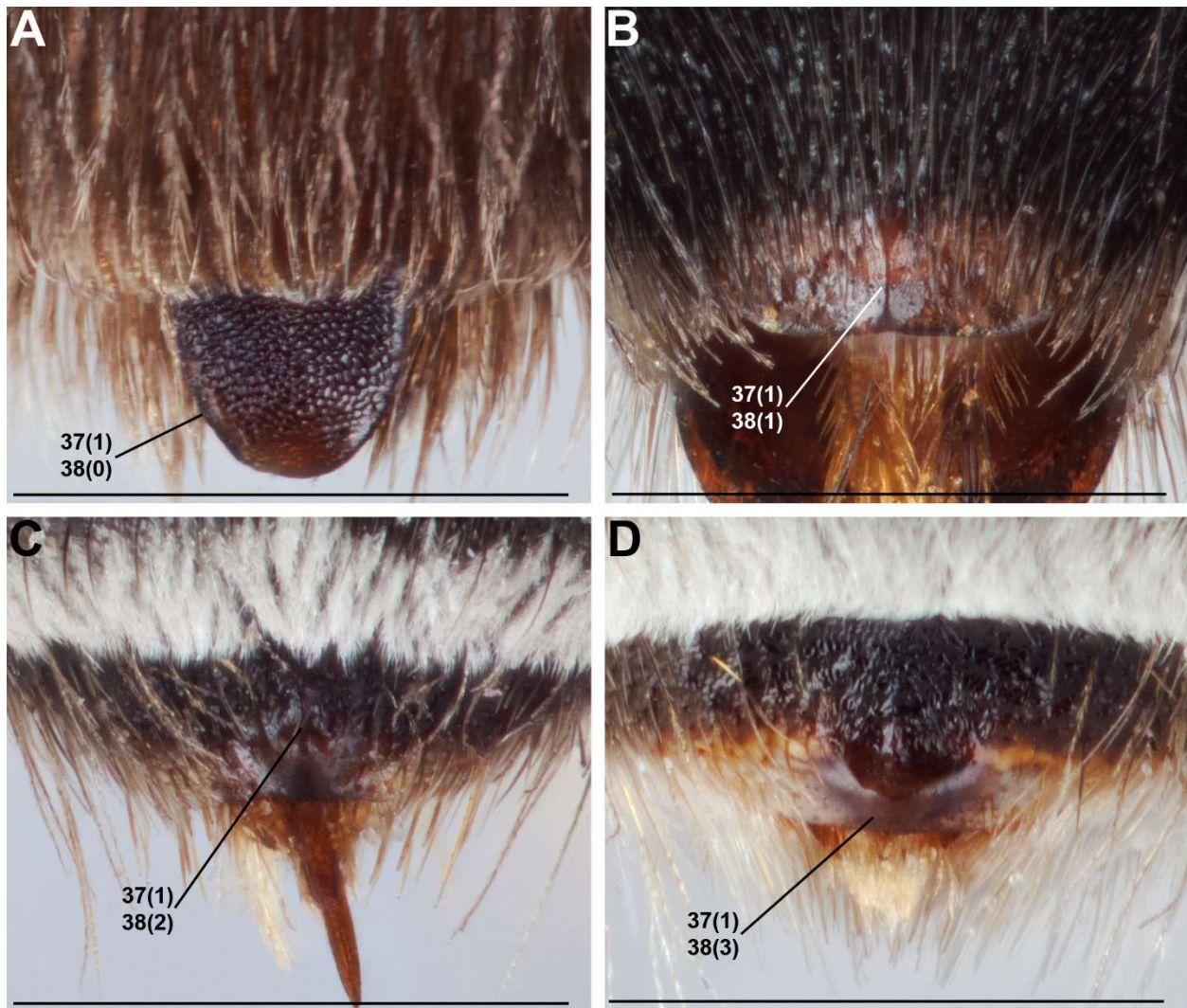
**51.** S6, posteromedial longitudinal ridge: (0) absent (Figs 17G–I,K,L); (1) present (Fig. 17J).

**52.** S6, shape of marginal zone: (0) entire (Fig. 17J); (1) emarginate medially (Figs 17I,K,L).

**53.** S6, shape of emargination of marginal zone: (0) weak (Figs 17I,K); (1) strong (Fig. 17L).

Not applicable for taxa coded as 52(0).





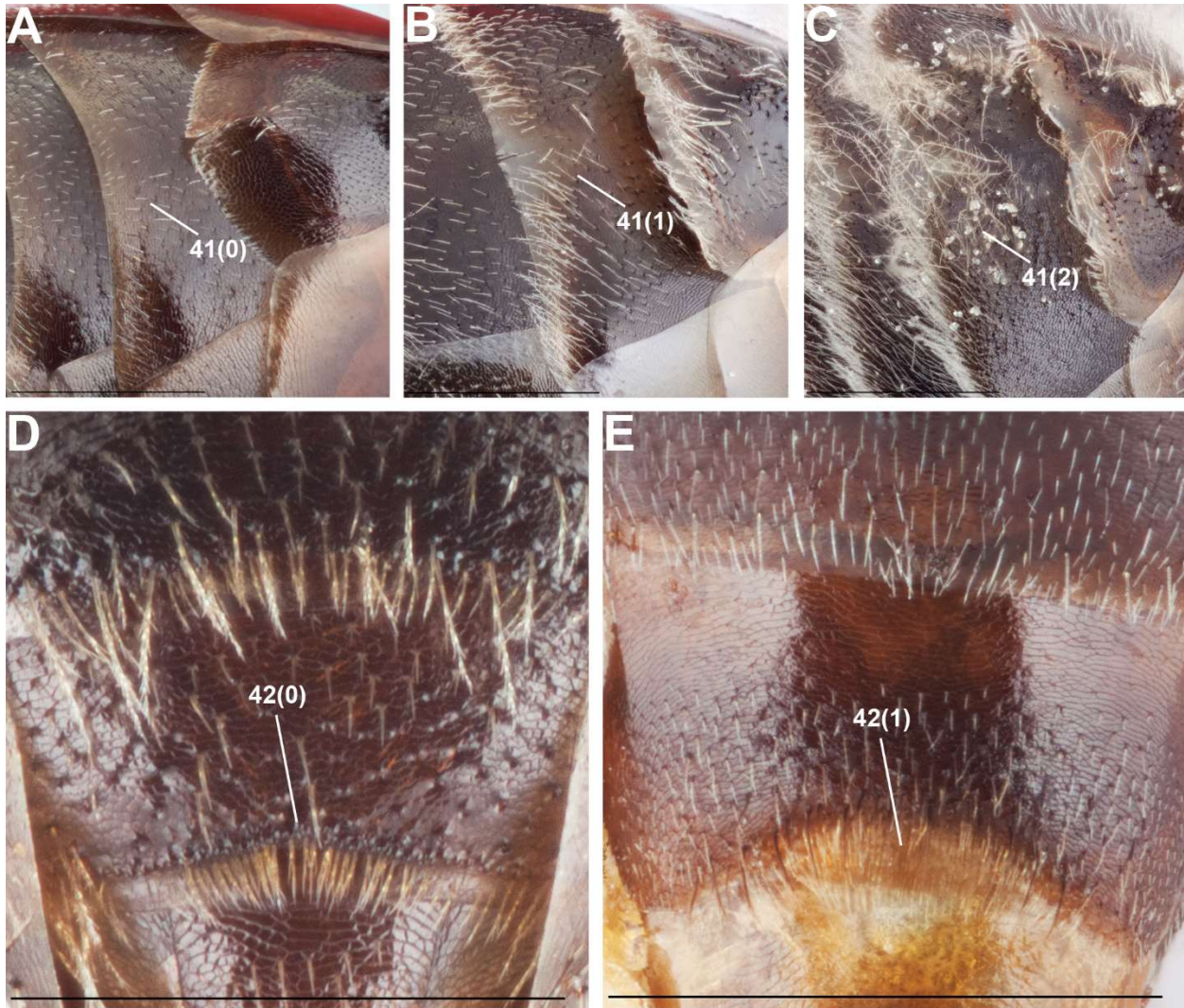
**Fig. 15.** Illustrations of states of characters 37 and 38. A-D, Dorsal view of female T6, *Bicolletes rufiventris* (A), *Hemicotelles ruizii* (B), *Xanthocotelles atacama* (C) and *X. incahuasi* (D). Scale bars = 1 mm.

### *Male*

**54.** Glossa, shape of apex: (0) bifid (Fig. 2B); (1) bilobed (Fig. 2A); (2) truncate (Michener, 2007: Fig. 47-1b).

**55.** Prementum, posterior surface, fovea: (0) absent; (1) present (Michener, 2007: Fig. 41-3).

**56.** Mandible, colour of proximal third: (0) dark-brown to black (Figs 8D,E); (1) pale-brown; (2) pale-yellow (Fig. 8F).



**Fig. 16.** Illustrations of states of characters 41 and 42. A-C, Lateroventral view of female S2, *Hylaeus modestus* (A), *Colletes gilvus* (B) and *Xanthocotelles atacama* (C); D,E, ventral view of female S5, *Scapter spinipes* (D) and *H. modestus* (E). Scale bars = 1 mm.

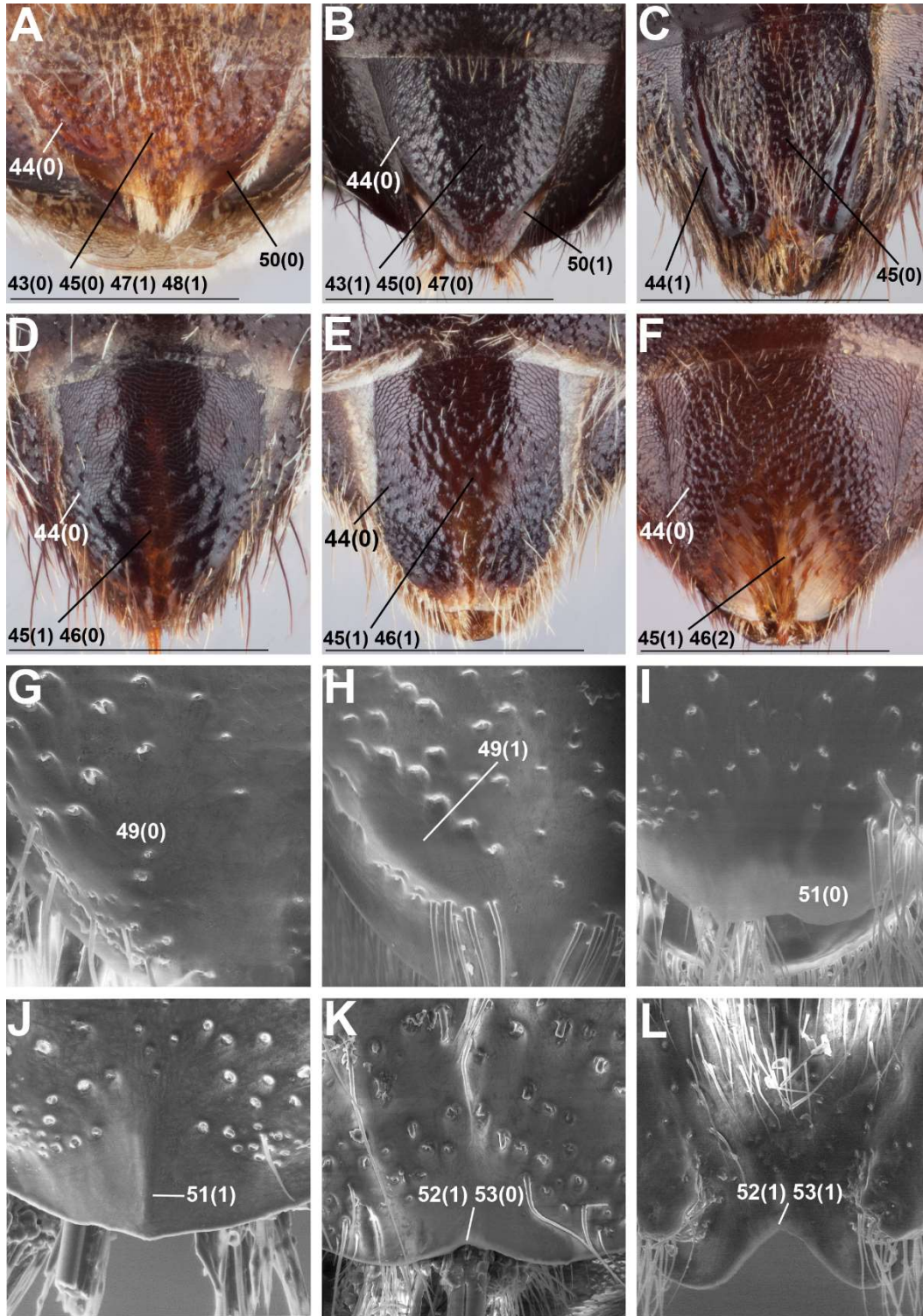
**57.** Mandible, apical tooth, shape of lower margin distally: (0) gently curved (Fig. 18A); (1) strongly curved (Fig. 18B).

**58.** Mandible, apical tooth, length in relation to preapical tooth: (0) only slightly longer (Fig. 18B); (1) much longer (Fig. 18A).

**59.** Mandible, preapical tooth, width in relation to apical tooth: (0) slightly narrower (Fig. 18B); (1) much narrower (Fig. 18A).

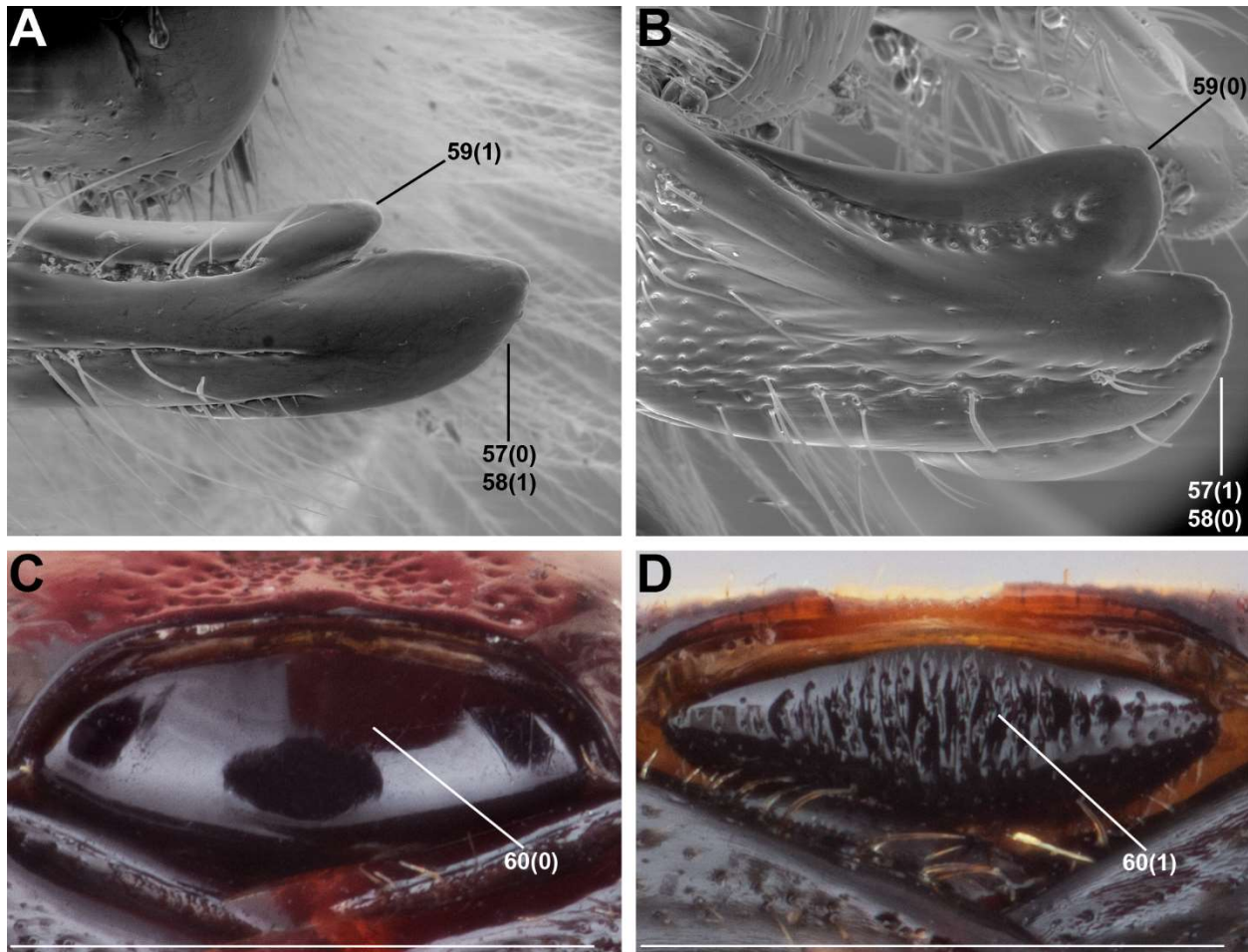
**60.** Labrum, punctation: (0) absent (Fig. 18C); (1) present (Fig. 18D).





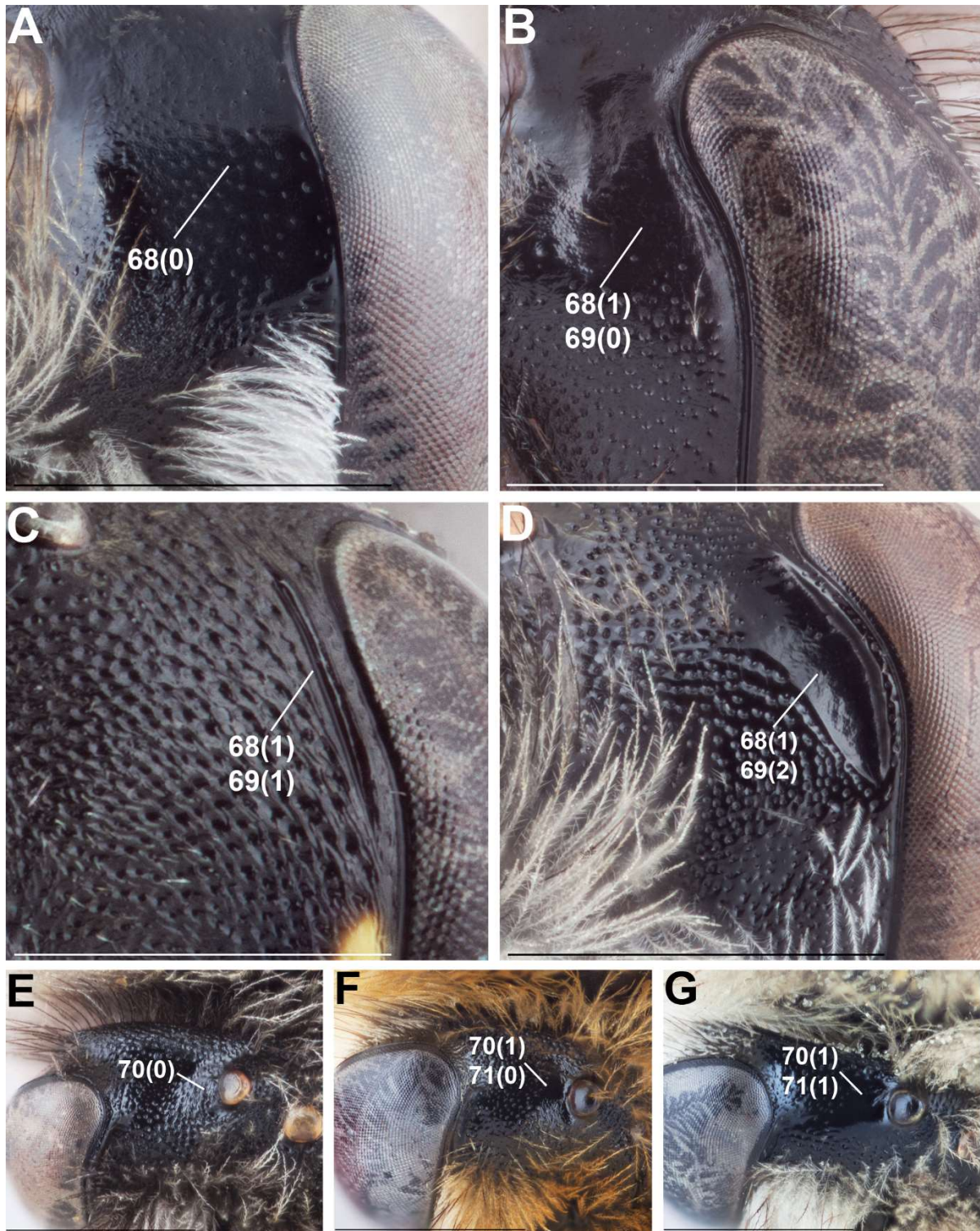
**Fig. 17.** Illustrations of states of characters 43–53. A–L, Ventral view of female S6, *Xanthocotelles sicheli* (A), *Mourecotelles mixtus* (B), *Colletes compactus* (C), *C. gilvus* (D), *C. coriandri* (E), *C. hyalinus* (F), *C. gilvus* (G), *C. rufipes* (H), *C. inexpectatus* (I), *C. cyanescens* (J), *C. inaequalis* (K) and *C. compactus* (L). Scale bars = 1 mm.





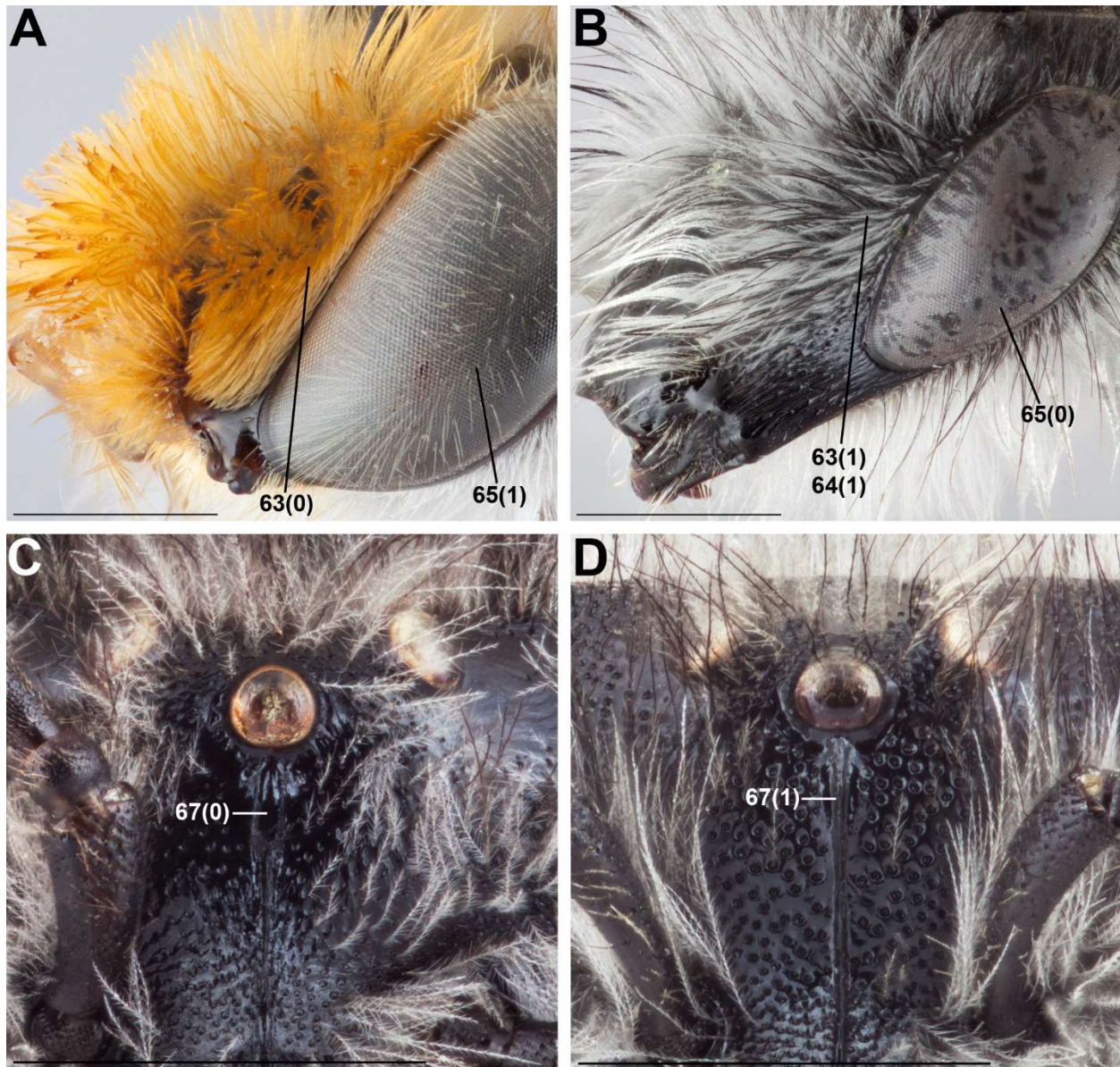
**Fig. 18.** Illustrations of states of characters 57–60. A,B, Outer view of male mandible, *Colletes gilvus* (A) and *Mourecotelles mixtus* (B); C,D, frontal view of male labrum, *C. atripes* (C) and *Hylaeus modestus* (D). Scale bars = 1 mm.

- 61.** Face, pale markings: (0) absent; (1) present.
- 62.** Clypeus, punctation of convex area: (0) sparse ( $i > 2d$ ; Figs 7A,B); (1) dense ( $i = 0.5–1.5d$ ; Fig. 6G); (2) very dense ( $i < 0.5d$ ; Figs 6E,F).
- 63.** Paraocular area, black hairs: (0) absent (Fig. 20A); (1) present (Fig. 20B).
- 64.** Paraocular area, distribution of black hairs: (0) sparse; (1) forming a dense longitudinal band (Fig. 20B). Not applicable for taxa coded as 63(0).
- 65.** Eye, length of hairs: (0) minute (Fig. 20B); (1) relatively long (Fig. 20A).
- 66.** Flagellum, colour of ventral surface: (0) dark-brown to black; (1) pale-brown; (2) yellow.
- 67.** Frontal line, shape of upper end: (0) sulcate (Fig. 20C); (1) carinate (Fig. 20D).



**Fig. 19.** Illustrations of states of characters 68–71. A–D, Frontal view of male upper paraocular area, *Trichocolletes dowerinensis* (A), *Mydrosoma sabarensis* (B), *Hylaeus modestus* (C) and *Colletes gilvus* (D); E–G, anterodorsal view of male vertexal area, *C. atripes* (E), *Xanthocotelles atacama* (F) and *Mourecotelles mixtus* (G). Scale bars = 1 mm.





**Fig. 20.** Illustrations of states of characters 63–65 and 67. A,B, Lateral view of male head, *Trichocolletes dowerinensis* (A) and *Colletes cyanescens* (B); C,D, frontal view of male frontal line, *Mourecotelles mixtus* (C) and *C. gilvus* (D). Scale bars = 1 mm.

**68.** Upper paraocular area, facial fovea: (0) absent (Fig. 19A); (1) present (Figs 19B–D).

**69.** Upper paraocular area, shape of facial fovea: (0) broad, shallow depression (Fig. 19B); (1) groove (Fig. 19C); (2) narrow, deep depression (Fig. 19D). Not applicable for taxa coded as 68(0).

- 70.** Vertexal area, impunctate smooth area lateral to lateral ocellus: (0) absent (Fig. 19E); (1) present (Figs 19F,G).
- 71.** Vertexal area, relative width of impunctate smooth area lateral to lateral ocellus: (0) small, at most  $0.5 \times \text{MOD}$  (Fig. 19F); (1) large, at least  $0.75 \times \text{MOD}$  (Fig. 19G). Not applicable for taxa coded as 70(0).
- 72.** Pronotum, shape of dorsolateral angle: (0) rounded (Fig. 21A); (1) obtusely angulate (Ferrari & Silveira, 2015: Fig. 2D); (2) acutely angulate (Ferrari & Silveira, 2015: Fig. 2C); (3) modified into a long spine (Fig. 21B).
- 73.** Mesoscutum, pubescence: (0) short and sparse; (1) long and dense (Fig. 1).
- 74.** Mesoscutum, black hairs: (0) absent (Figs 1A,B,D,E,F,I,J,N,O,P); (1) present (Figs 1C,G,H,K,L,M).
- 75.** Mesoscutum, distribution of black hairs: (0) relatively sparse (Figs 1C,G,L); (1) pubescence entirely black (Figs 1H,K,M). Not applicable for taxa coded as 74(0).
- 76.** Tegula, colour: (0) dark-brown to black (Ferrari, 2017: Fig. 51F); (1) pale-brown (Ferrari, 2017: Fig. 54F); (2) pale-yellow (Ferrari, 2017: Fig. 28F).
- 77.** Scutellum, shape in posterodorsal view: (0) flat (Figs 21C,E,F); (1) concave (Fig. 21D).
- 78.** Scutellum, colour of pubescence: (0) off-white (Ferrari, 2017: Fig. 4F); (1) pale-yellow (Ferrari, 2017: Fig. 24F); (2) pale-yellow and fuscous intermixed (Ferrari, 2017: Fig. 13F); (3) dark-orange (Ferrari, 2017: Fig. 28F); (4) black (Ferrari, 2017: Fig. 49F); (5) black and off-white intermixed (Ferrari, 2017: Fig. 40F).
- 79.** Scutellum, posterolateral strong hook-like projection: (0) absent (Figs 21C–E); (1) present (Fig. 21F).
- 80.** Hypoepimeral area, impunctate band below: (0) absent (Fig. 22D); (1) present (Figs 22B,C).
- 81.** Mesepisternum, punctures: (0) minute (Fig. 22A); (1) fine (Fig. 22B); (2) coarse (Fig. 22C); (3) very coarse (Fig. 22D).
- 82.** Mesepisternum, punctation: (0) sparse ( $i > 2d$ ; Fig. 22A); (1) moderately sparse ( $i = 1–1.5d$ ; Fig. 22B); (2) dense ( $i = 0.5–1.0d$ ; Fig. 22C); (3) very dense ( $i < 0.5d$ ; Fig. 22D).
- 83.** Mesepisternum, microsculpture of interspaces: (0) smooth (Figs 22B,C); (1) imbricate (Fig. 22A); (2) rugose (Fig. 22D).
- 84.** Metepisternum, microsculpture of upper protuberance: (0) smooth (Fig. 23A); (1) imbricate (Fig. 23B); (2) rugulose (Fig. 23C); (3) rugose (Fig. 23D); (4) areolate (Fig. 23E).

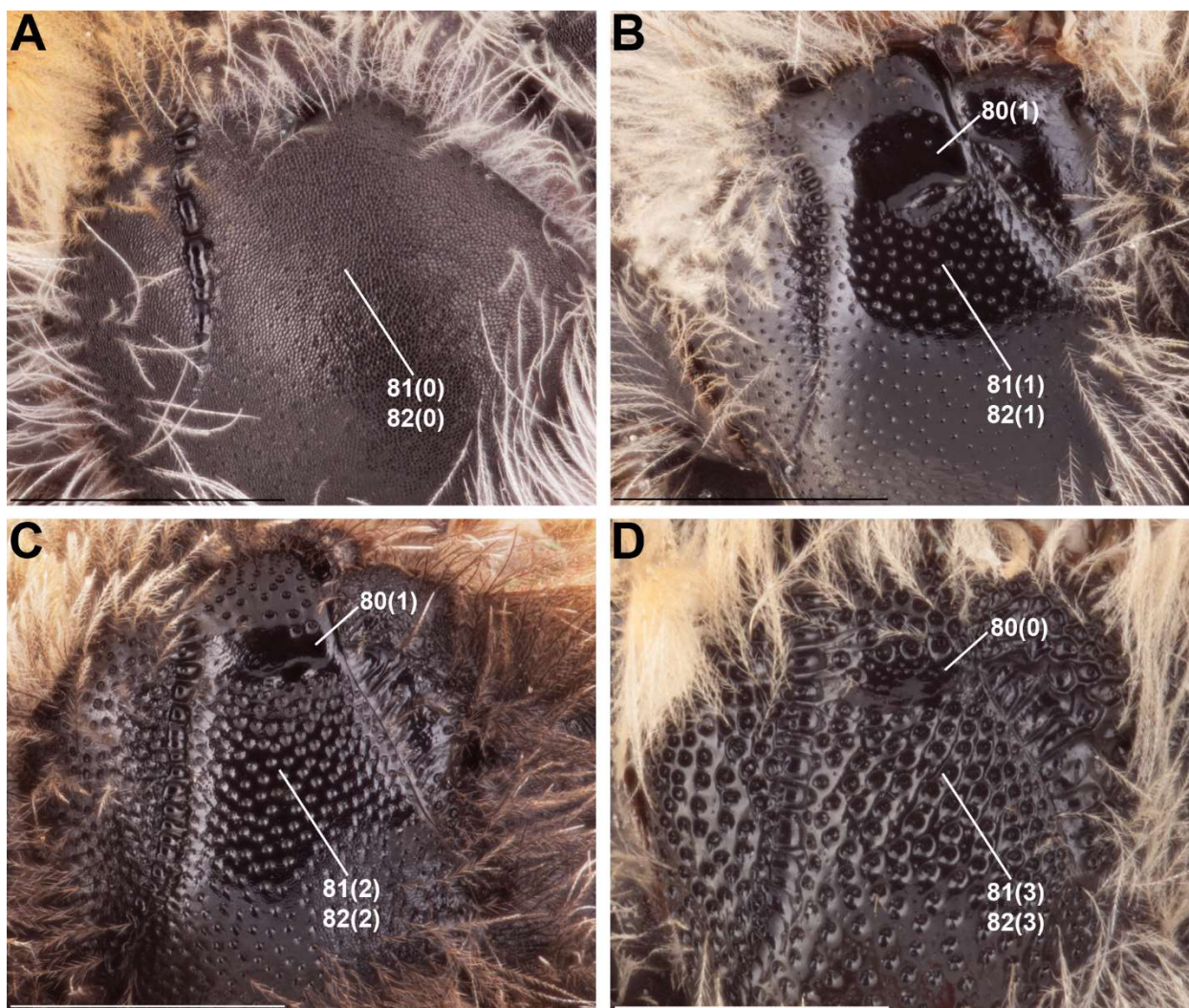




**Fig. 21.** Illustrations of states of characters 72, 77 and 79. A,B, Anterior view of male pronotum, *Mourecotelles mixtus* (A) and *Colletes simulans* (B); C-F, dorsal view of male scutellum, *C. halophilus* (C), *C. nasutus* (D), *C. validus* (E) and *C. nasutus* (F).

Scale bars = 1 mm.





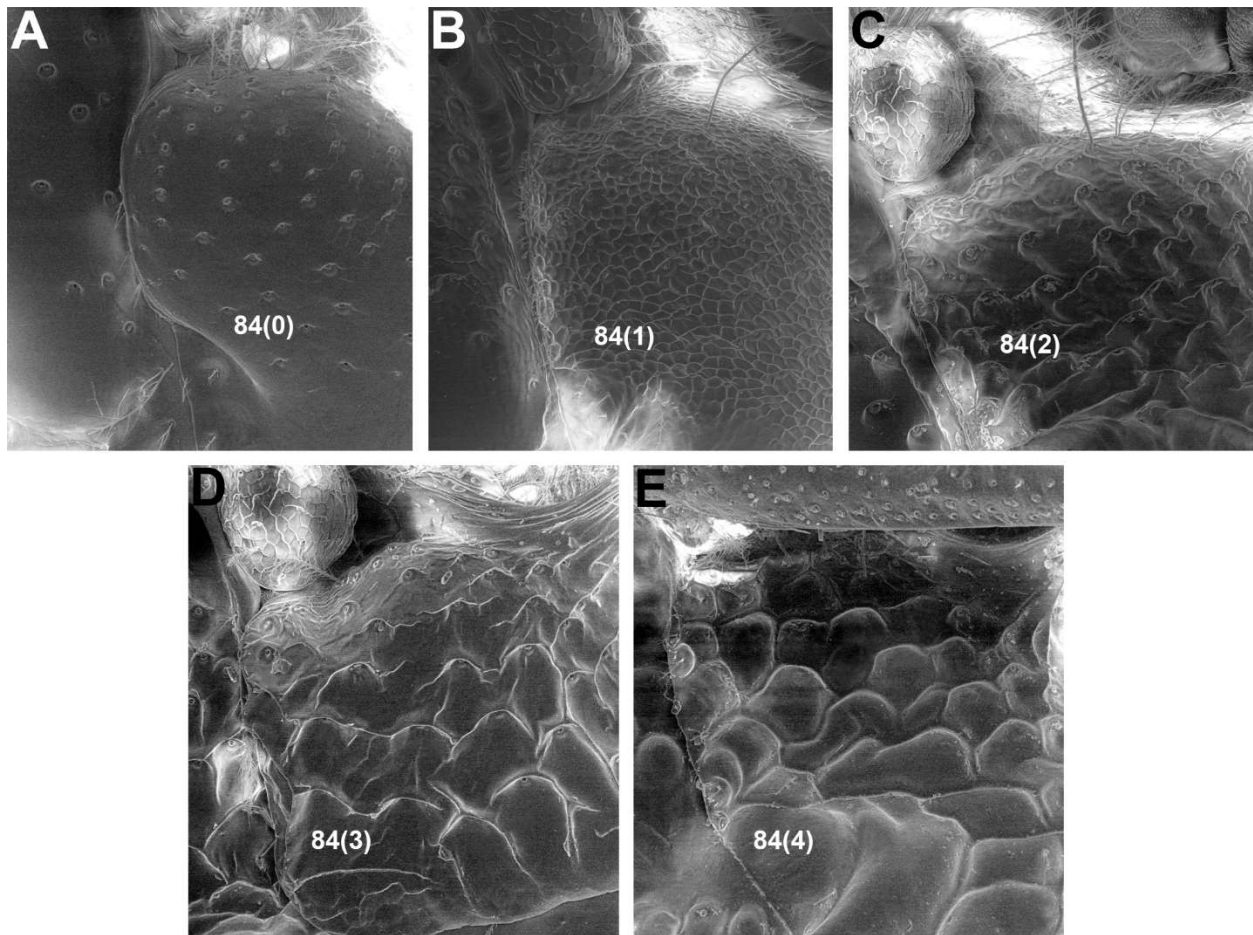
**Fig. 22.** Illustrations of states of characters 80–82. A–D, Lateral view of male mesepisternum, *Trichocolletes dowerinensis* (A), *Mourecotelles mixtus* (B), *Colletes atripes* (C) and *C. eous* (D). Scale bars = 1 mm.

**85.** Metepisternum, upper protuberance, pale-brown transverse lamella below: (0) absent (Figs 24A–C); (1) present (Fig. 24D).

**86.** Metepisternum, oblique striae below upper protuberance: (0) absent (Fig. 24A); (1) present (Figs 24B–D).

**87.** Metepisternum, strength of oblique striae: (0) weak, poorly indicated (Fig. 24B); (1) strong, very distinct (Figs 24C,D). Not applicable for taxa coded as 86(0).

**88.** Metapostnotum, subhorizontal surface: (0) absent (Fig. 4A); (1) present (Fig. 4B).



**Fig. 23.** Illustrations of states of character 84. A-E, Scanning electron micrographs of male metepisternum, *Mourecotelles mixtus* (A), *Colletes cyanescens* (B), *C. atripes* (C), *C. americanus* (D) and *C. eous* (E). Scale bars = 1 mm.

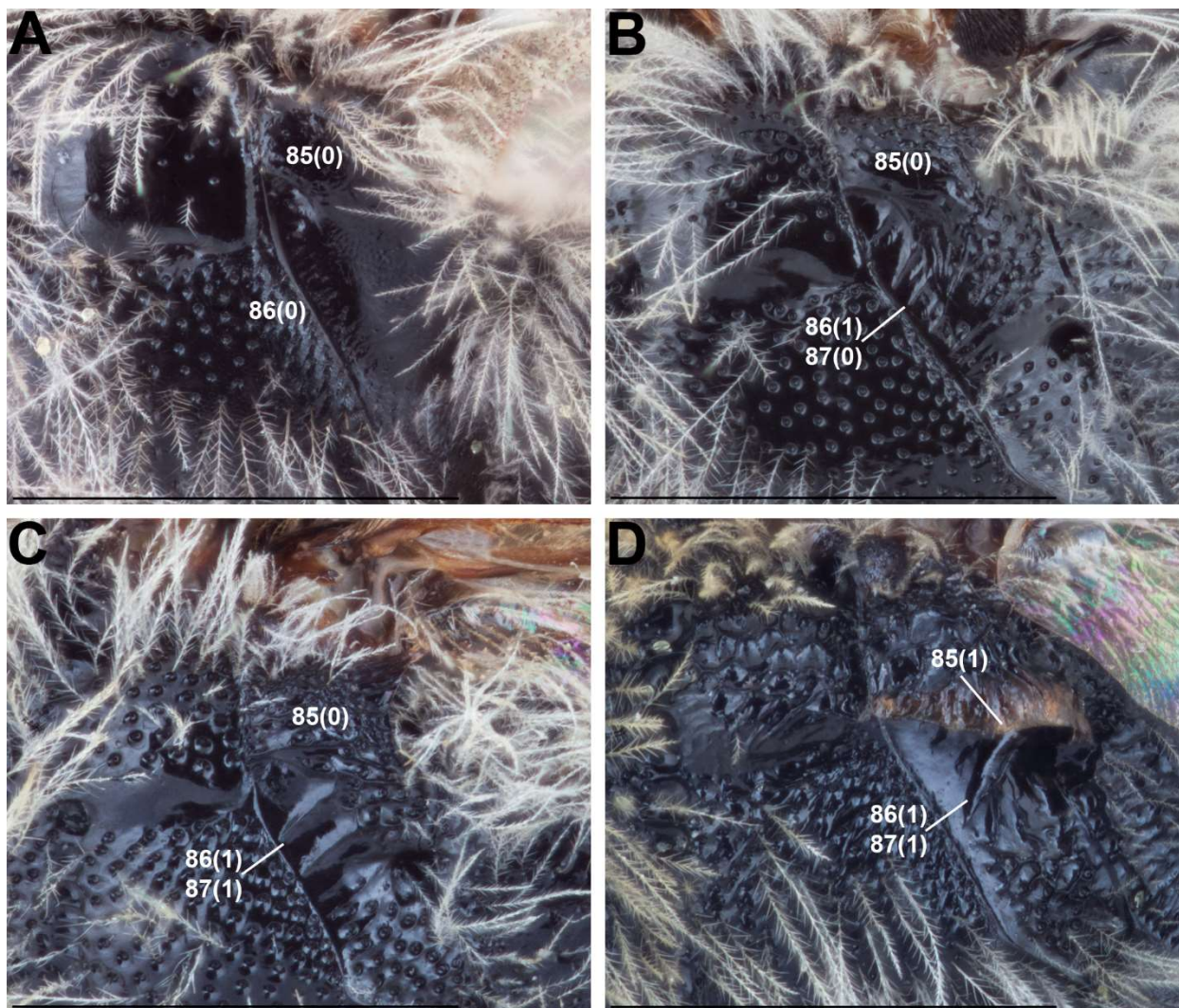
**89.** Metapostnotum, subhorizontal surface, longitudinal carinae: (0) absent (Figs 4C,D); (1) present (Fig. 4E). Not applicable for taxa coded as 88(0).

**90.** Metapostnotum, junction between subhorizontal and vertical surfaces, transverse carina: (0) absent (Fig. 4C); (1) present (Figs 4D,E).

**91.** Metapostnotum, junction between subhorizontal and vertical surfaces, length of transverse carina: (0) interrupted medially (Fig. 4D); (1) complete (Fig. 4E). Only applicable for taxa coded as 88(1) and 90(1).

**92.** Lateral surface of propodeum, punctures: (0) minute (Fig. 4A); (1) fine (Fig. 4B); (2) coarse.





**Fig. 24.** Illustrations of states of characters 85–87. A–D, Lateral view of male metepisternum, *Mourecotelles mixtus* (A), *Colletes gilvus* (B), *C. slevini* (C) and *C. americanus* (D). Scale bars = 1 mm.

**93.** Lateral surface of propodeum, microsculpture of interspaces: (0) imbricate (Fig. 4A); (1) smooth (Fig. 4B); (2) rugulose (as in Fig. 23C); (3) rugose (as in Fig. 23D).

**94.** Forewing, colour of membrane: (0) hyaline (Figs 3A,B); (1) yellowish (Fig. 3D); (2) dusky (Fig. 3C).

**95.** Forewing, number of submarginal cells: (0) 2 (Fig. 3A); (1) 3 (Figs 3B–D).

**96.** Forewing, shape of vein 2m-cu: (0) straight (Figs 3A,B); (1) slightly arcuate outwardly (Fig. 3C); (2) sigmoidal (Fig. 3D).

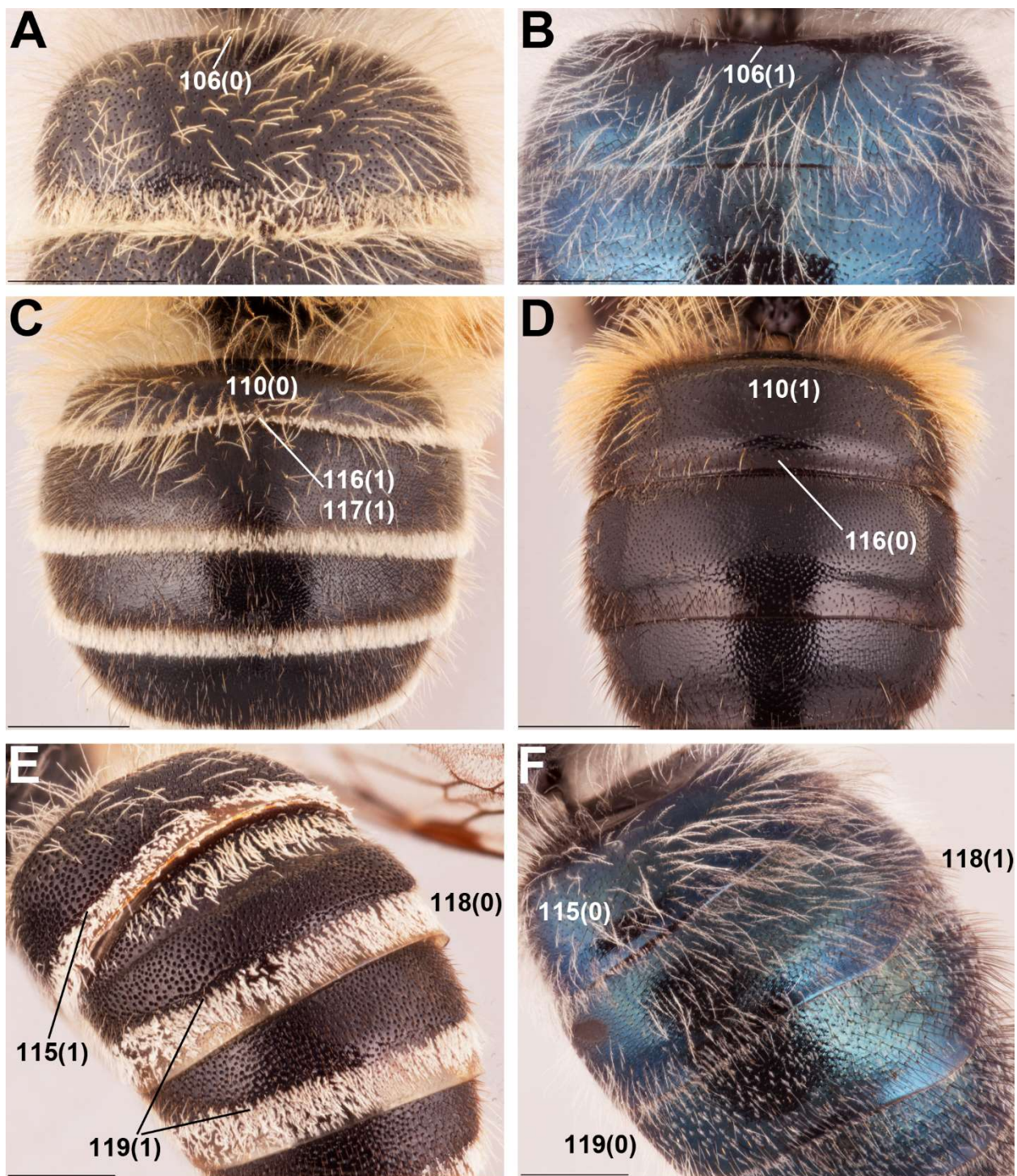


- 97.** Tibiae, colour: (0) dark-brown to black (Fig. 12H); (1) pale-yellow to pale-brown (Fig. 12G).
- 98.** Front tibia, anterior surface proximally, pale marking: (0) absent (Fig. 25A); (1) present (Fig. 25B).
- 99.** Hind trochanter, ventral spine: (0) absent (Fig. 25C); (1) present (Fig. 25D).
- 100.** Hind tibia, basitibial plate: (0) absent (Fig. 2C); (1) present (Fig. 2D).
- 101.** Hind tibia, anteroventral surface distally, strong process: (0) absent (Fig. 25E); (1) present (Fig. 25F).
- 102.** Hind tibial spurs, colour: (0) pale-yellow (Fig. 12F); (1) pale-brown (Fig. 12D); (2) dark-brown to black (Fig. 12E).
- 103.** Hind basitarsus, shape of anterior surface proximally: (0) entire (Fig. 25G); (1) emarginate (Fig. 25H).
- 104.** Hind tarsomere 2, posterodistal corner, process: (0) absent (Fig. 25I); (1) present (Figs 25J–N).
- 105.** Hind tarsomere 2, shape of posterodistal process: (0) broadly rounded (Fig. 25J); (1) narrowly rounded (Fig. 25K); (2) right angle (Fig. 25L); (3) acute angle (Fig. 25M); (4) long subcylindrical lobe (Fig. 25N). Not applicable for taxa coded as 104(0).
- 106.** T1, anterior margin, shape in anterior view: (0) flat (Figs 26A,E); (1) concave (Figs 26B,F).
- 107.** T1, anterior declivous surface, medial longitudinal depression: (0) absent; (1) present.
- 108.** T1, anterior declivous surface, shape of anterior medial longitudinal depression: (0) narrow groove; (1) a broad deep depression. Not applicable for taxa coded as 107(0).
- 109.** T1, anterior declivous surface, relative length of broad deep depression: (0) relatively short, barely surpassing midlength of anterior surface; (1) relatively long, almost reaching junction between anterior and dorsal surfaces. Only applicable for taxa coded as 107(1) and 108(1).
- 110.** T1, dorsal surface, relative length in relation to T2 dorsal surface: (0) much shorter (Fig. 26C); (1) subequal (Fig. 26D).
- 111.** T1, dorsal surface, type of hair: (0) simple; (1) branched (Fig. 11A).
- 112.** T1, dorsal surface, colour of hairs: (0) off-white (Figs 26B,E,F); (1) pale-yellow (Figs 26A,C); (2) pale-orange (Fig. 26D); (3) black.
- 113.** T1, dorsal surface, punctures medially: (0) minute (Figs 26B,C); (1) fine (Figs 26A,D); (2) coarse; (3) very coarse (Fig. 26E).



**Fig. 25.** Illustrations of states of characters 98, 99, 101 and 103–105. A,B, Anterior view of male front tibia, *Colletes gilvus* (A) and *Mourecotelles mixtus* (B); C,D, anterior view of male hind trochanter, *C. gilvus* (C) and *Trichocolletes dowerinensis* (D); E,F, anterior view of male hind tibia, *C. nigrifrons* (E) and *Scapter papkuilsi* (F); G,H, outer view of male hind basitarsus, *Xanthocolletes atacama* (G) and *X. aisen* (H); I–N, outer view of male hind tarsomere 2, *C. atripes* (I), *C. impunctatus* (J), *Mourecotelles* sp. (L), *X. tarsalis* (M) and *C. albicinctus* (N). Scale bars = 1 mm.

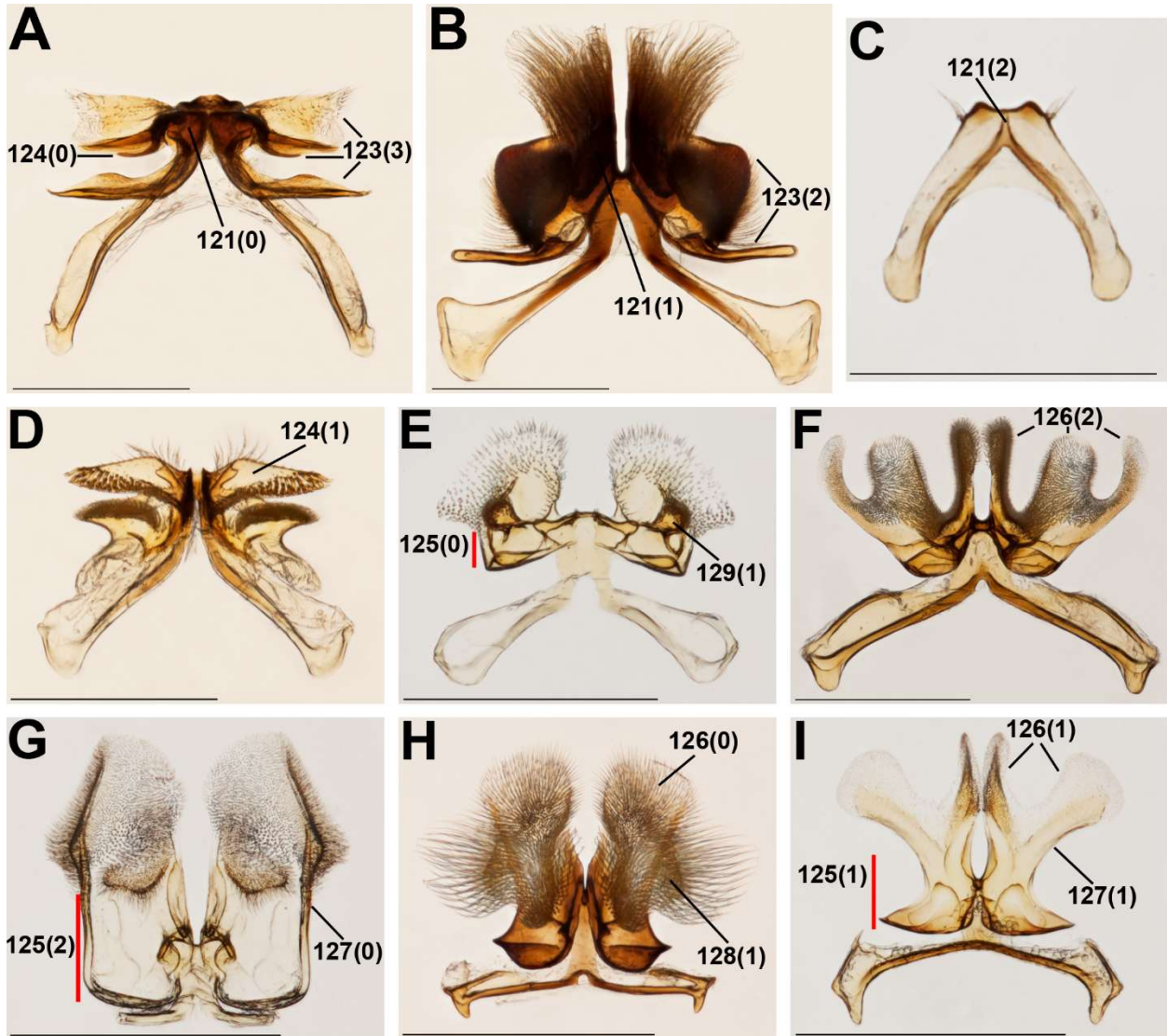




**Fig. 26.** Illustrations of states of characters 106, 110 and 115–119. A–D, Dorsal view of male metasoma, *Colletes gilvus* (A), *C. cyanescens* (B), *Xanthocotelles atacama* (C) and *C. atripes* (D); E, F, laterodorsal view of metasoma, *C. eous* (E) and *C. cyanescens* (F). Scale bars = 1 mm.

- 114.** T1, dorsal surface, punctation medially: (0) sparse ( $i > 2d$ ); (1) moderately sparse ( $i = 1-1.5d$ ); (2) dense ( $i = 0.5-1.0d$ ); (3) very dense ( $i < 0.5d$ ).
- 115.** T1, premarginal line: (0) poorly indicated (Fig. 26F); (1) very distinct (Fig. 26E).
- 116.** T1, marginal zone, tomentum band: (0) absent (Figs 26B,D,F); (1) present (Figs 26A,C,E).
- 117.** T1, marginal zone, length of tomentum band longitudinally: (0) incomplete, interrupted medially; (1) complete (Figs 26A,C,E). Not applicable for taxa coded as 116(0).
- 118.** T1–T5, metallic-blue reflections: (0) absent (Figs 26A,C,D,E); (1) present (Figs 26B,F).
- 119.** T2–T3, premarginal line: (0) poorly indicated (Fig. 26F); (1) very distinct (Fig. 26E).
- 120.** T3–T7, marginal zones, tomentum bands present on: (0) no terga; (1) T3; (2) T3 and T4; (3) T3–T5; (4) T3–T6; (5) T3–T7.
- 121.** S7, disc, shape: (0) subcircular (Fig. 27A); (1) bilobed and elongate (Fig. 27B); (2) reduced to a narrow bridge (Fig. 27C); (3) subpentagonal (Figs 27E–I).
- 122.** S7, apicolateral lobes: (0) absent (Fig. 27C); (1) present (Figs 27A,B,D–I).
- 123.** S7, number of apicolateral lobes: (0) 1 (Figs 27E–I); (1) 2 (Figs 27B,D); (2) 3 (Fig. 27A). Not applicable for taxa coded as 122(0).
- 124.** S7, shape of posterior apicolateral lobe: (0) slender (Fig. 27A); (1) subtriangular (Fig. 27D); (2) chevron-shaped; (3) remarkably enlarged posteriorly (Figs 27E–I). Not applicable for taxa coded as 122(0).
- 125.** S7, enlarged apicolateral lobe, relative length of neck in relation to S7 disc: (0) much shorter (Figs 27E,F,H); (1) subequal (Fig. 27I); (2) much longer (Fig. 27G). Only applicable for taxa coded as 122(1) and 124(3).
- 126.** S7, enlarged apicolateral lobe, shape of disc: (0) simple (Figs 27E,G,H); (1) bilobed (Fig. 27I); (2) trilobed (Fig. 27F). Only applicable for taxa coded as 122(1) and 124(3).
- 127.** S7, enlarged apicolateral lobe, disc, shape of lateral margin anteriorly: (0) straight (Figs 27F–H); (1) concave (Figs 27E,I). Only applicable for taxa coded as 122(1) and 124(3).
- 128.** S7, enlarged apicolateral lobe, disc, lateral expansion: (0) absent (Figs 27E–G,I); (1) present (Fig. 27H). Only applicable for taxa coded as 122(1) and 124(3).
- 129.** S7, enlarged apicolateral lobe, disc, ventral rounded protrusion: (0) absent (Figs 27F–I); (1) present (Fig. 27E). Only applicable for taxa coded as 122(1) and 124(3).
- 130.** S8, spiculum: (0) absent (Figs 28A,B); (1) present (Figs 28C–F).

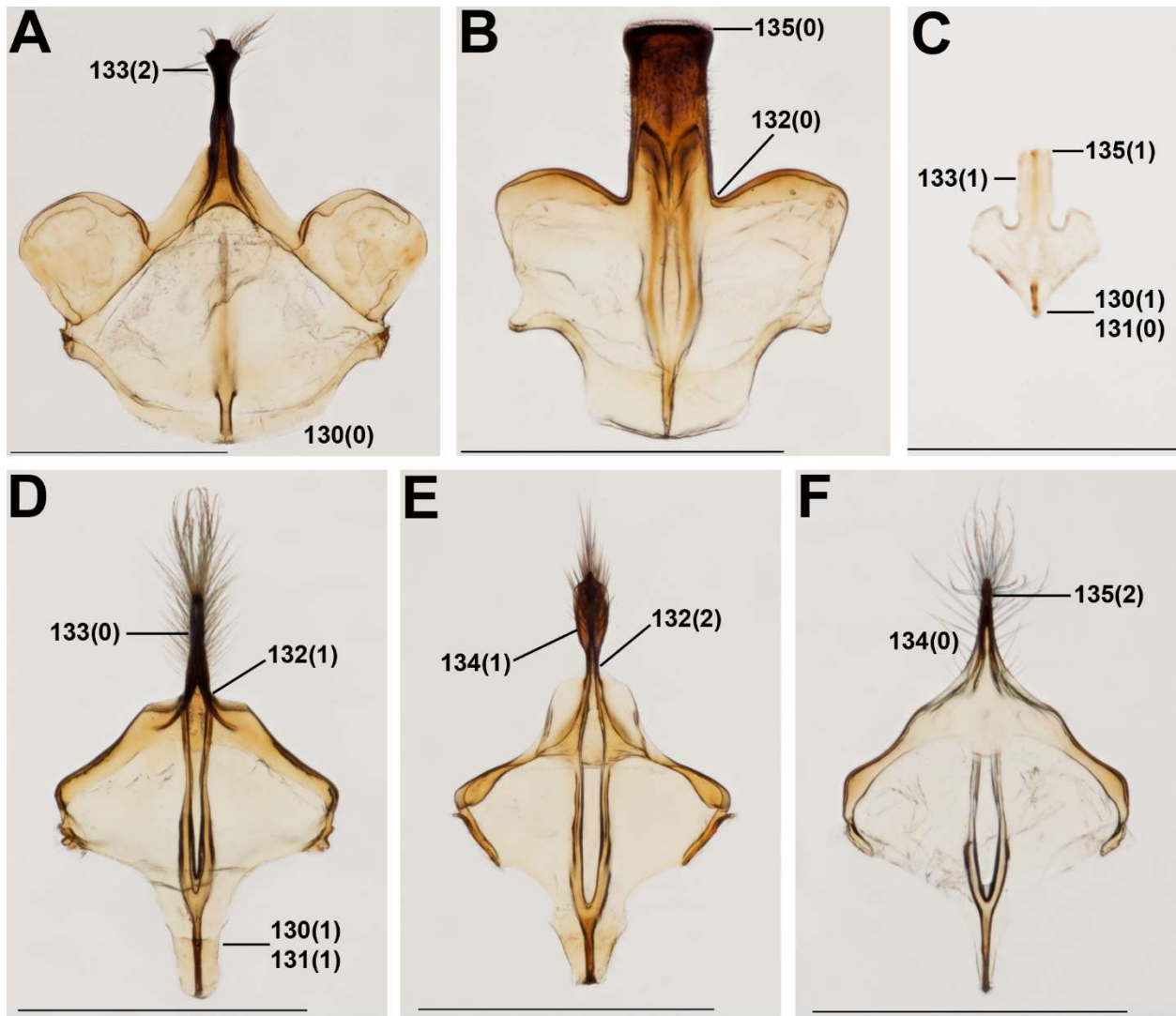




**Fig. 27.** Illustrations of states of characters 121 and 123–129. A–I, Ventral view of male S7, *Mydrosoma sabarensis* (A), *Trichocolletes dowerinensis* (B), *Scapter spinipes* (C), *Hexanthesa entrerriana* (D), *Xanthocotelles sicheli* (E), *C. inaequalis* (F), *C. chusmiza* (G), *C. hirtibasis* (H) and *C. kozlovi* (I). Red bars represent length of corresponding neck. Scale bars = 1 mm.

**131.** S8, length of spiculum in relation to disc: (0) much shorter (Fig. 28C); (1) subequal (Figs 28D–F). Not applicable for taxa coded as 130(0).

**132.** S8, posterolateral margin, angle with distal process: (0) acute (Figs 28B,C); (1) right angle (Fig. 28D); (2) obtuse (Figs 28A,E,F).

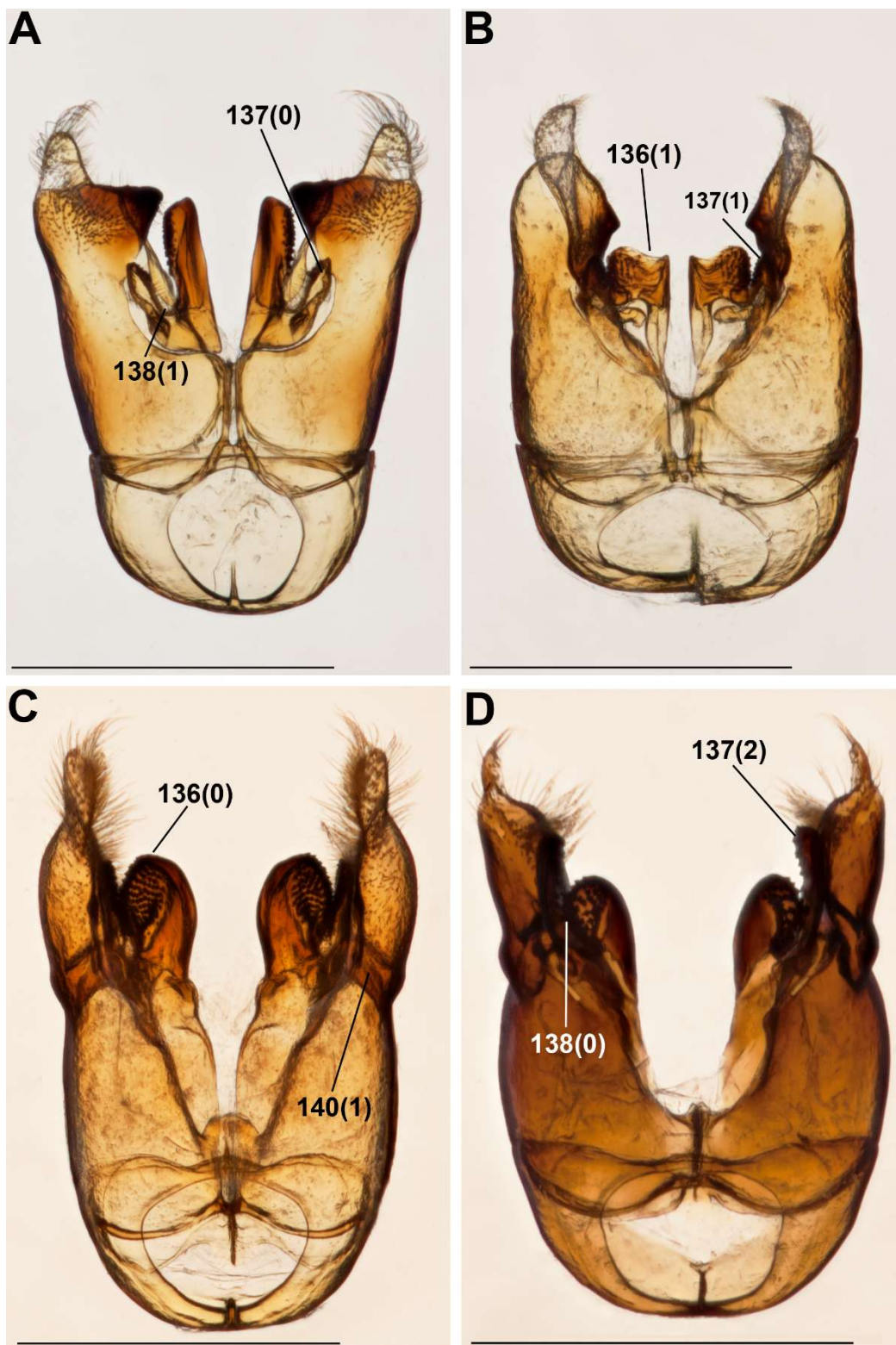


**Fig. 28.** Illustrations of states of characters 130–135. A–F, Dorsal view of male S8, *Mydrosoma sabarensis* (A), *Hexanthesa entrerriana* (B), *Chilicola herbsti* (C), *Hemicotelles ruizii* (D), *Colletes bombiformis* (E) and *C. simulans* (F). Scale bars = 1 mm.

**133.** S8, shape distal process: (0) narrow throughout (Figs 28D,F); (1) broad throughout (Fig. 28C); (2) broadening distad (Figs 28A,B,E).

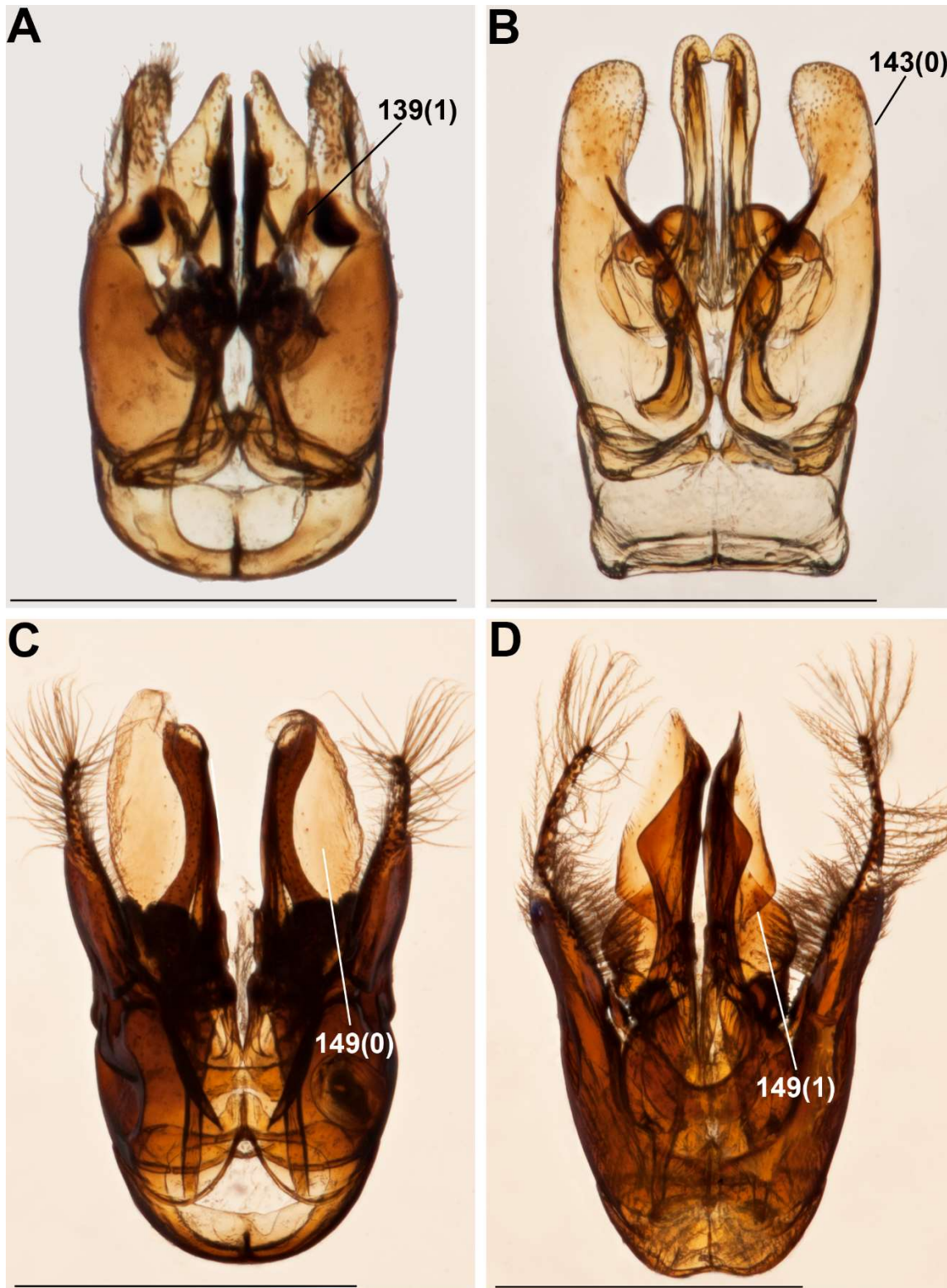
**134.** S8, distal process, lateral expansion: (0) absent (Figs 28D,F); (1) present (Fig. 28E). Not applicable for taxa coded as 133(0).

**135.** S8, distal process, shape of apex in dorsal view: (0) rounded (Fig. 28B); (1) truncate (Fig. 28C); (2) pointed (Figs 28D–F).



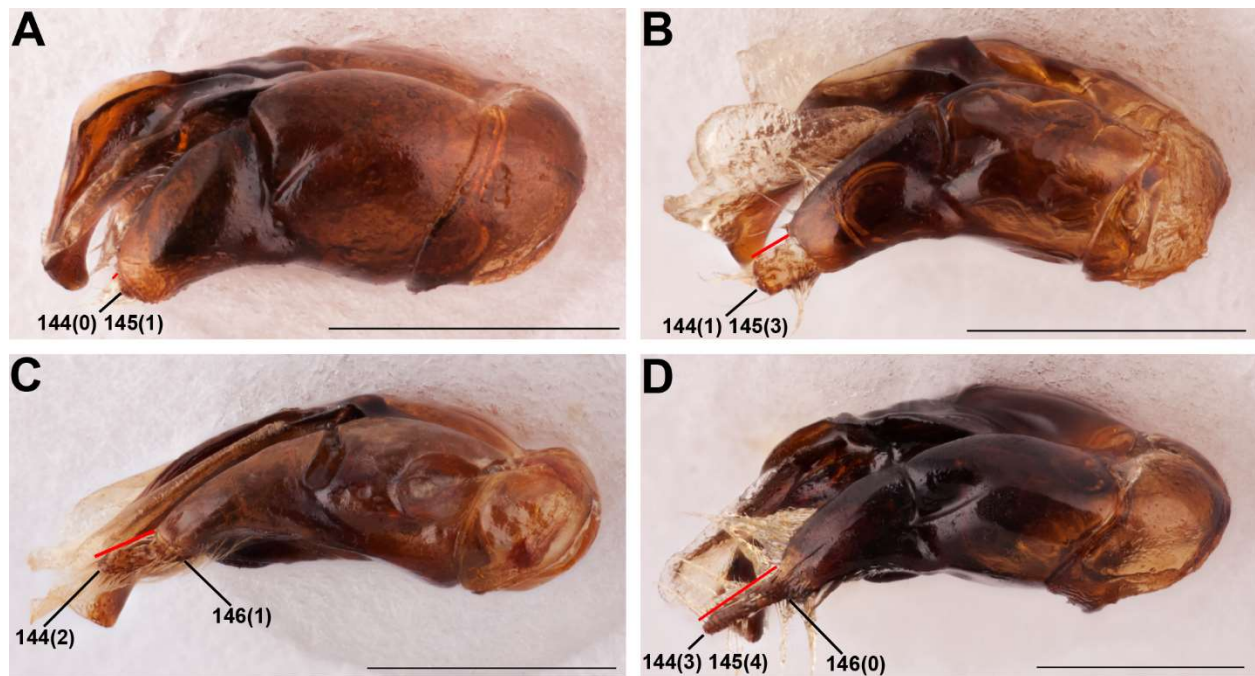
**Fig. 29.** Illustrations of states of characters 136–138 and 140. A–D, Dorsal view of male genital capsule, *Xanthocotelles atacama* (A), *Mourecotelles mixtus* (B), *Colletes atripes* (C) and *C. inexpectatus* (D). Scale bars = 1 mm.





**Fig. 30.** Illustrations of states of characters 139, 143 and 149. A-D, Dorsal view of male genital capsule, *Scrapter spinipes* (A), *Hylaeus modestus* (B), *Colletes capensis* (C) and *C. eous* (D). Scale bars = 1 mm.





**Fig. 31.** Illustrations of states of characters 144–146. A,D, Lateral view of male genital capsule, *Colletes eulophi* (A), *C. coriandri* (B), *C. albomaculatus* (C) and *C. nasutus* (D). Red bars represent length of corresponding gonostylus. Scale bars = 1 mm.

**136.** Volsella, digitus, shape of apex: (0) convex (Figs 29A,C,D); (1) concave (Fig. 29B).

**137.** Volsella, relative length of cuspis in relation to digitus: (0) much shorter (Fig. 29A); (1) subequal (Figs 29B,C); (2) much longer (Fig. 29D).

**138.** Volsella, separation between cuspis and digitus: (0) very narrow (Figs 29B–D); (1) broad (Fig. 29A).

**139.** Gonocoxa anteroventral strong process: (0) absent (Figs 30B–D); (1) present (Fig. 30A).

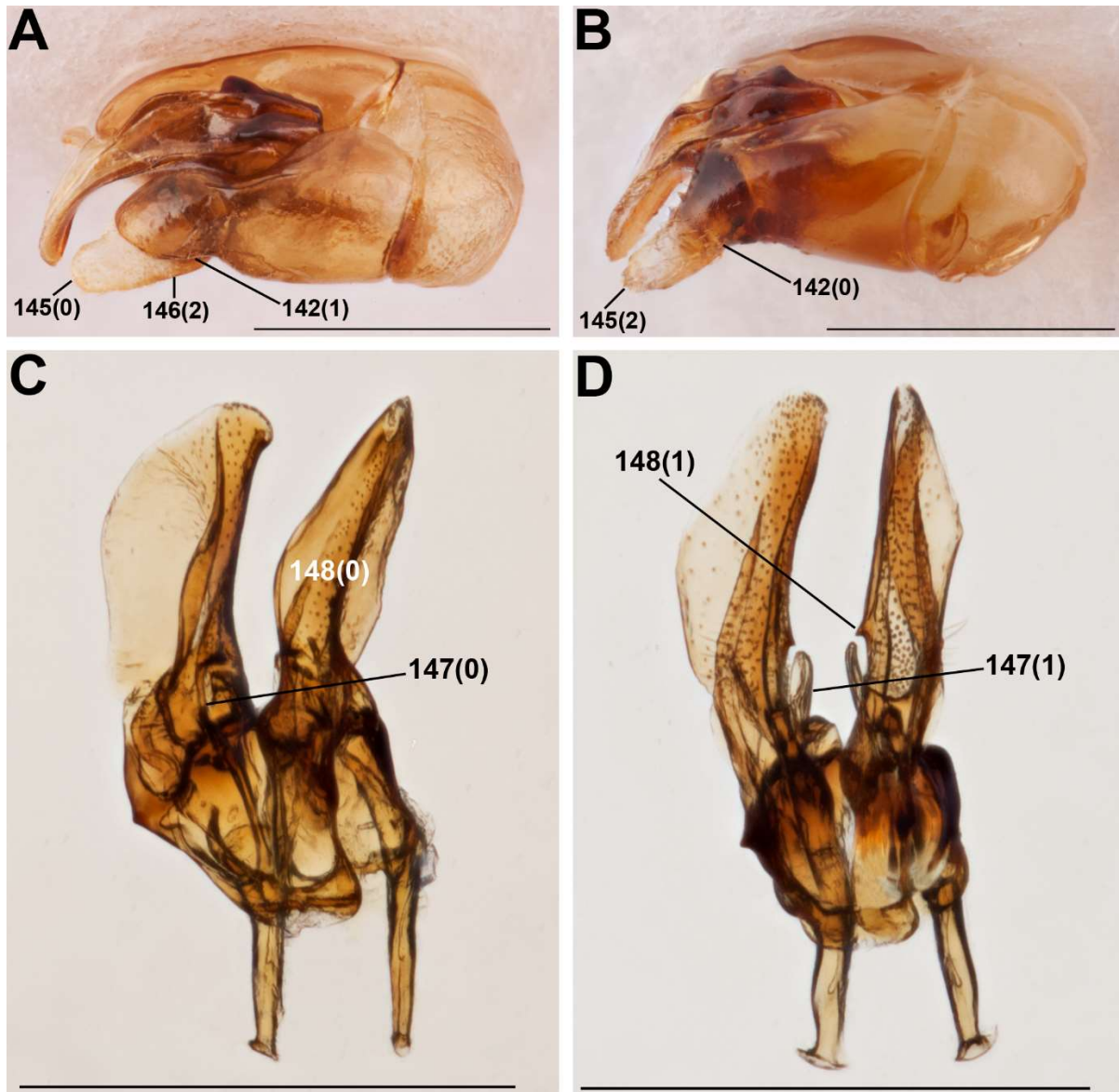
**140.** Gonocoxa, dorsomedial transverse deep sulcus: (0) absent (Figs 29A,B); (1) present (Figs 29C,D).

**141.** Gonocoxa, posteroventral tubercle: (0) absent (Figs 29C,D); (1) present (Figs 29A,B).

**142.** Gonocoxa, dorsoventrally oriented deep sulcus separating apex from gonostylus: (0) absent (Fig. 32B); (1) present (Fig. 32A).

**143.** Gonostylus: (0) undifferentiated from gonocoxa (Fig. 30B); (1) distinct (Figs 30A,C,D).

**144.** Gonostylus, length in lateral view: (0) tiny (Fig. 31A); (1) short (Fig. 31B); (2) long (Fig. 31C); (3) very long (Fig. 31D). Not applicable for taxa coded as 143(0).

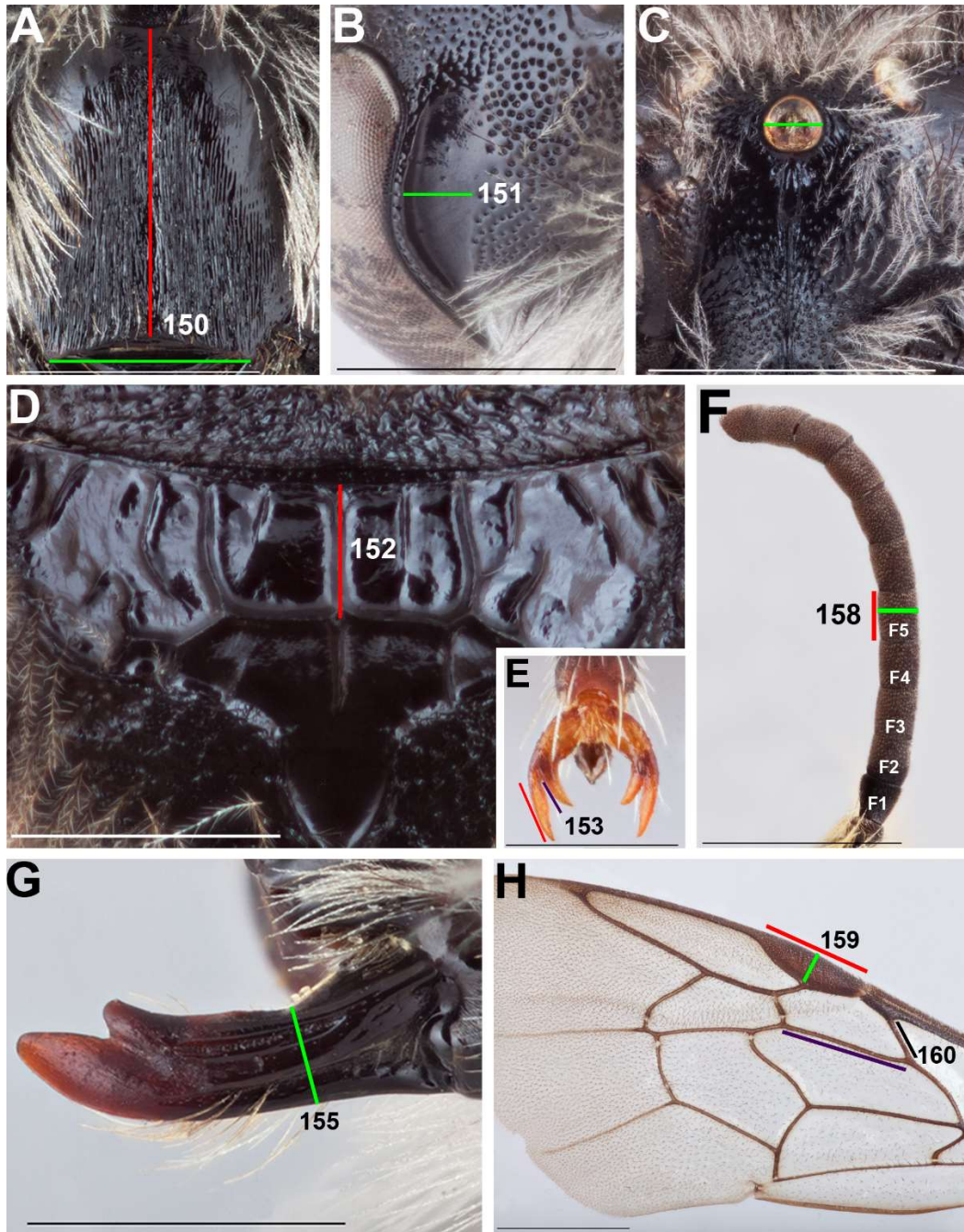


**Fig. 32.** Illustrations of states of characters 142, 144–148. A,B, Lateral view of male genital capsule, *Mourecotelles spinolae* (A) and *Xanthocotelles fritzi* (B); C,D, dorsal view of male penis valves, *Colletes americanus* (C) and *C. gilvus* (D). Scale bars = 1 mm.

**145.** Gonostylus, shape in lateral view: (0) broadly rounded (Fig. 32A); (1) arrowhead-shaped (Fig. 31A); (2) narrowly rounded (Fig. 32B); (3) subrectangular (Fig. 31B); (4) spiniform (Fig. 31D). Not applicable for taxa coded as 143(0).

**146.** Gonostylus, base width in relation to gonocoxa apex: (0) narrower (Fig. 31D); (1) subequal (Fig. 31C); (2) broader (Fig. 32A). Not applicable for taxa coded as 143(0).





**Fig. 33.** Indication on how the continuous characters were measured. A, Length (red bar) and apical width (green bar) of female clypeus; B, maximum width (green bar) of female facial fovea; C, diameter (green bar) of female median ocellus; D, length (red bar) of subhorizontal surface of female metapostnotum; E, length of apical (red bar) and subapical (purple bar) teeth of female hind tarsal claws; F, length (red bar) and mid width (green bar) of male F5; G, mid width (green bar) of male mandible; H, length (red bar) and maximum width (green bar) of male pterostigma and lengths of male veins Rs+M (purple bar) and Rs (black bar). Scale bars = 1 mm.

- 147.** Apodeme of penis valve, shape of apex: (0) broad and flat (Fig. 32C); (1) modified as subcylindrical lobe directed posteriorly (Fig. 32D).
- 148.** Penis valve, dorsal wing, medial spine: (0) absent (Fig. 32C); (1) present (Fig. 32D).
- 149.** Penis valve, shape of ventral wing: (0) entire (Fig. 30C); (1) bilobed (Fig. 30D).

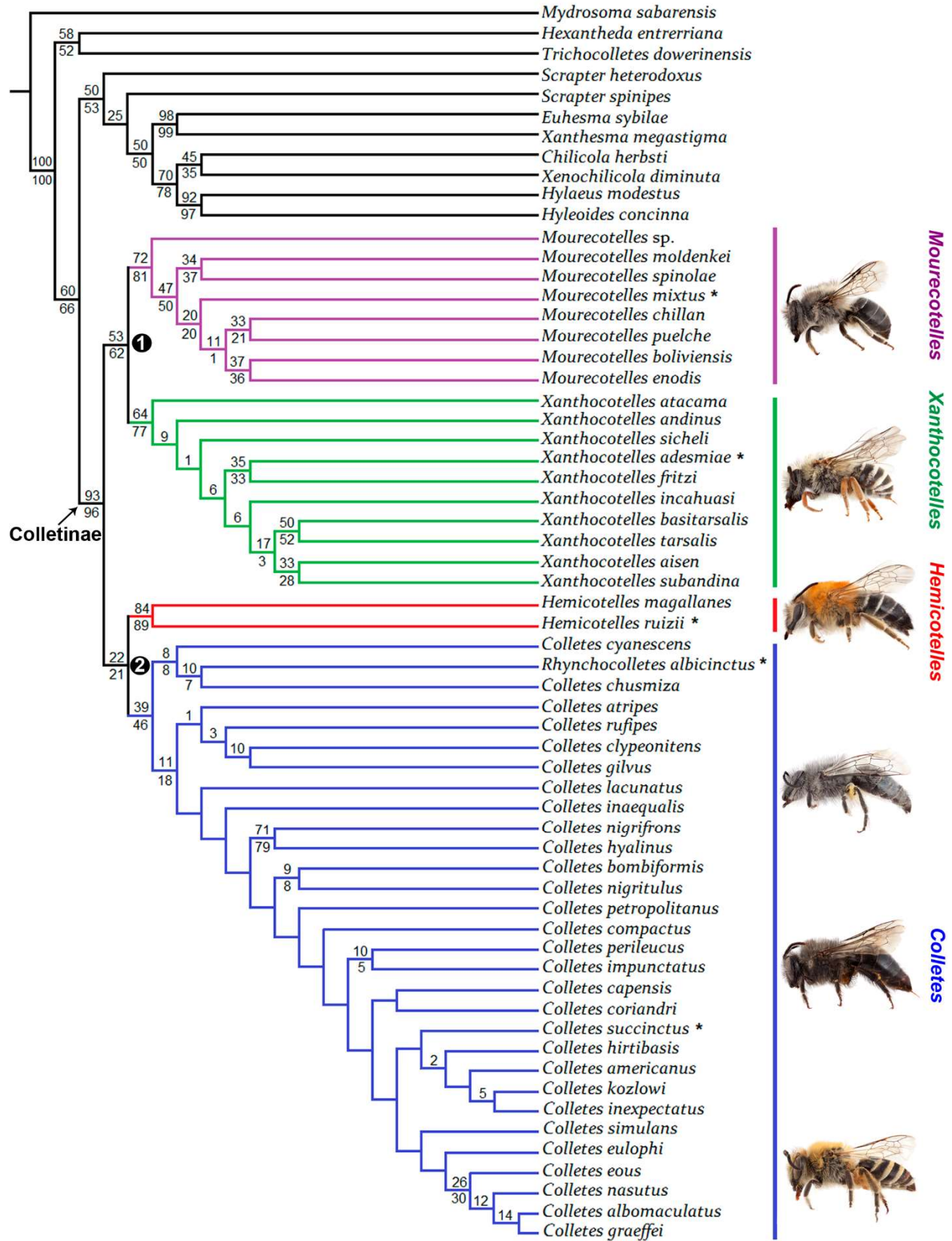
#### *Continuous*

- 150.** Female, ratio between clypeus length and apical width (Fig. 33A).
- 151.** Female, ratio between facial fovea maximum width and MOD (Figs 33B,C).
- 152.** Female, ratio between length of subhorizontal surface of metapostnotum and MOD (Figs 33C,D).
- 153.** Female, hind tarsal claws, ratio between lengths of apical and subapical teeth (Fig. 33E).
- 154.** Male, head width (Ferrari, 2017: Fig. 65C).
- 155.** Male, ratio between mandible mid width and MOD (Figs 33C,G).
- 156.** Male, ratio between malar area length and width (Ferrari, 2017: Fig. 65A).
- 157.** Male, ratio between F1 length and apical width (Ferrari, 2017: Fig. 65B).
- 158.** Male, ratio between F5 length and mid width (Fig. 33F).
- 159.** Male, ratio between pterostigma length and maximum width (Fig. 33H).
- 160.** Male, ratio between forewing veins Rs+M and Rs lengths (Fig. 33H).
- 161.** Male, ratio between hind basitarsus length and mid width (Ferrari, 2017: Fig. 65D).

#### *Phylogenetic results*

The EW analysis yielded a single most parsimonious tree (Fig. 34) with 902.74 steps (CI = 25.2 and RI = 65.6). The IW analysis also resulted in a single tree (Fig. 35) with total fit of 72.48 (CI = 24.4 and RI = 64.0). Both analyses show that Colletinae is monophyletic and strongly supported (GC and BS > 90) by our data. The subfamily is defined by 13 synapomorphies, four of which are unique and located in the hidden metasomal sterna of the males: S7 with (i) a reduced subpentagonal disc and (ii) remarkably enlarged apicolateral lobes (Fig. 4F); and S8 possessing (iii) a narrow distal process with (iv) a pointed apex (Figs 28D–F).



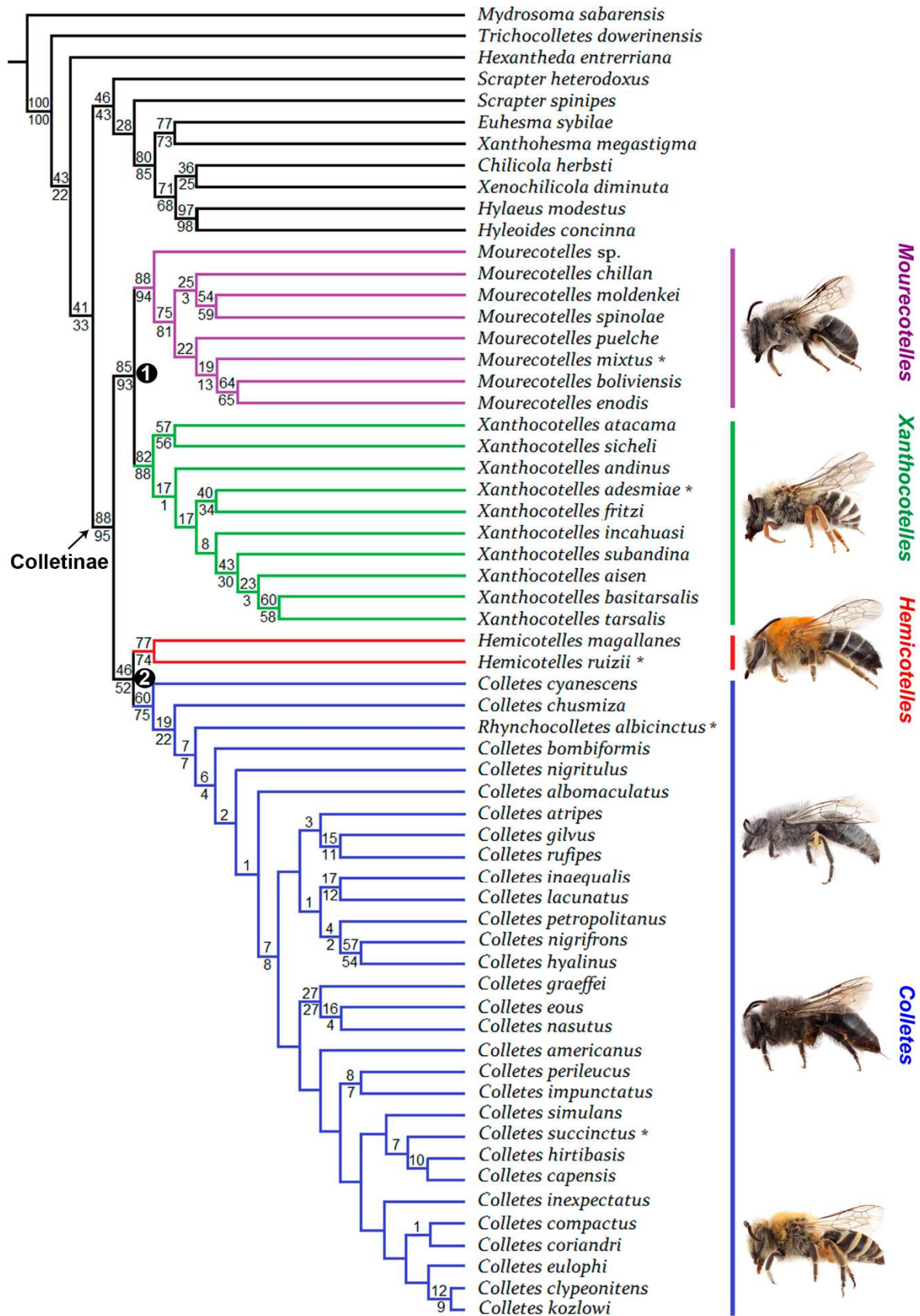


**Fig. 34.** Most parsimonious tree from the EW analysis of the combined data. Numbers above internodes are absolute values from bootstrapping and below are GC ratios (negative values not shown) from symmetric resampling. Asterisks indicate type species of the genus. The Colletinae shown are (from top to bottom) *Mourecotelles mixtus*, *Xanthocotelles fritzi*, *Hemicotelles ruizii*, *Colletes cyanescens*, *C. nigrifolius* and *C. halophilus*.

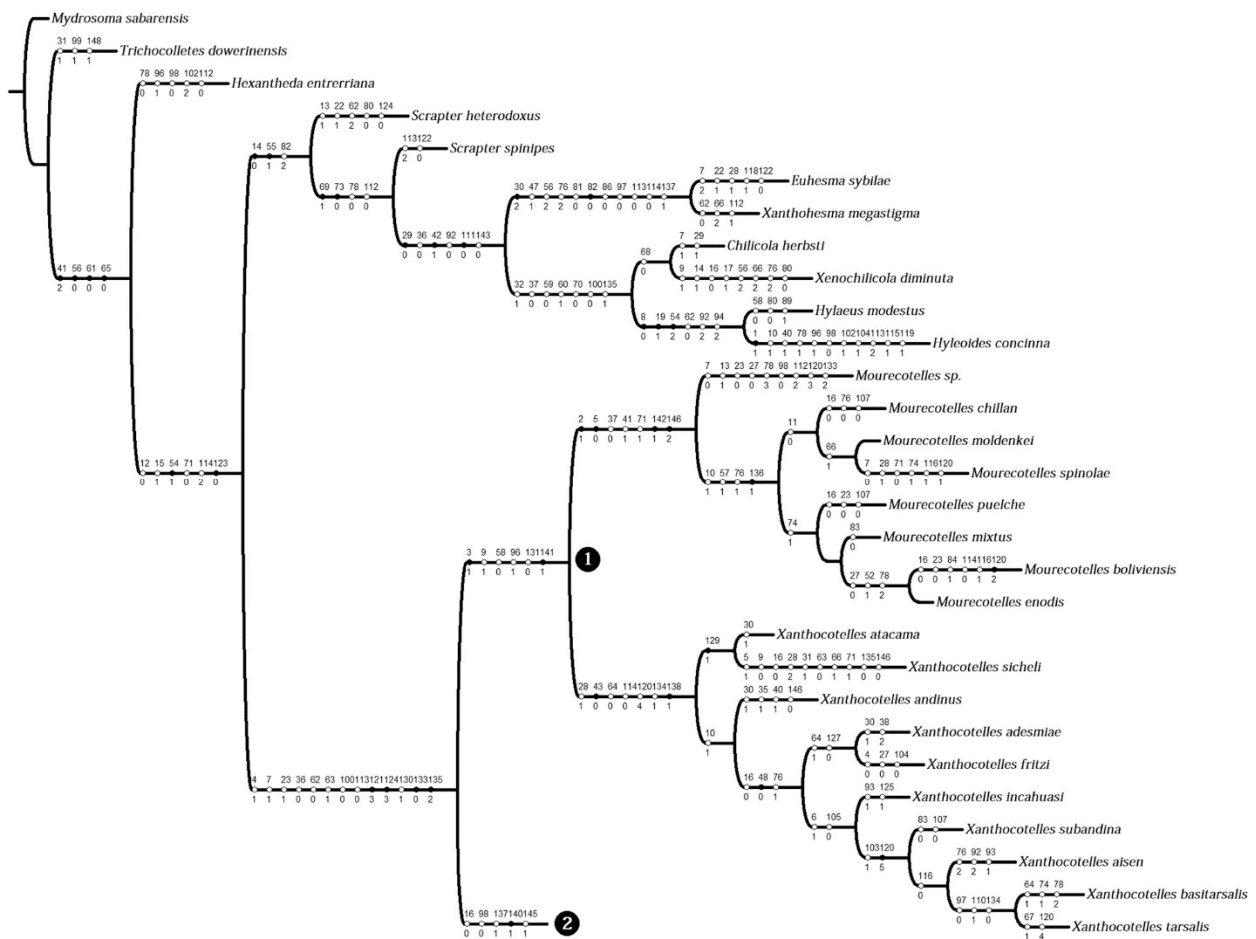
The fittest tree from the IW analysis showing all character state changes mapped onto it is presented in Figs 36, 37.

The higher-level relationships within Colletinae are identical between the two analyses, and both show that the subfamily consists of two major clades (see Figs 34, 35). ‘Clade 1’ includes the reciprocally monophyletic *Mourecotelles* s.str. and *Xanthocotelles* which are linked by two unique synapomorphies: (i) apical and preapical mandibular teeth forming a right angle in the females (Fig. 5F); and (ii) gonocoxa bearing a posteroventral tubercle in the males (Figs 29A,B). ‘Clade 1’ is strongly supported by the IW analysis (GC = 93, BS = 85), but somewhat less so by the EW one (GC = 62, BS = 53). ‘Clade 2’ contains the genera *Hemicotelles* and *Colletes*, which are reciprocally monophyletic, and is supported by five synapomorphies, including gonocoxa with a transverse deep sulcus dorsoposteriorly which is unique (Figs 29C,D), and is moderately well supported by the IW analysis (GC = 52, BS = 46), but significantly less so by the EW one (GC = 21, BS = 22). *Rynchocolletes albicinctus* belongs to an early branch within *Colletes* according to both EW and IW analyses.

As delimited herein, *Mourecotelles* s.str. is supported by seven synapomorphies, four of them unique: (i) preapical mandibular tooth truncate (Fig. 5D), and (ii) labrum with longitudinal median ridge (Fig. 6A) in the females; (iii) apex of gonocoxa narrower than base of gonostylus and (iv) bearing a dorsoventrally-oriented sulcus (Fig. 32A) in the males. Monophyly of the genus is relatively strongly supported by both IW (GC = 88, BS = 82) and EW (GC = 77, BS = 64) analyses. The relationships within *Mourecotelles* s.str. are significantly discrepant between the two analyses, however, both show that *Mourecotelles* sp. from southeastern Brazil is sister to all of its congeners.

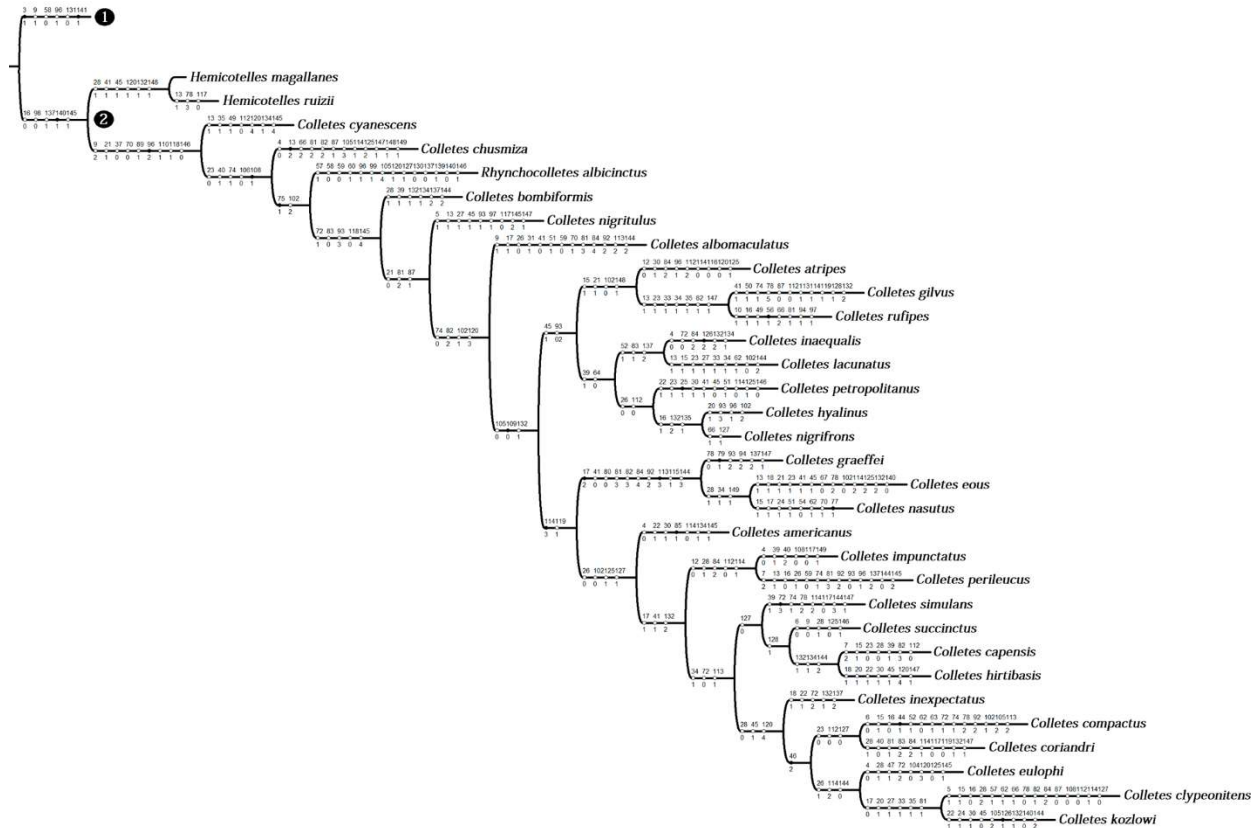


**Fig. 35.** Fittest tree from the IW analysis of the combined data. Numbers above internodes are absolute values from bootstrapping and below are GC ratios (negative values not shown) from symmetric resampling. Asterisks indicate type species of the genus. The Colletinae shown are (from top to bottom) *Mourecotelles mixtus*, *Xanthocotelles fritzi*, *Hemicotelles ruizii*, *Colletes cyanescens*, *C. nigrifolius* and *C. halophilus*.



**Fig. 36.** Fittest tree (part one) with the character state changes mapped onto it. Black circles represent unique changes and white circles represent homoplastic ones. Character numbers are indicated above branches and the corresponding state changes below the branches.





**Fig. 37.** Fittest tree (part two) with the character state changes mapped onto it. Black circles represent unique changes and white circles represent homoplastic ones. Character numbers are indicated above branches and the corresponding state changes below the branches.

*Xanthocotelles* is supported by seven synapomorphies, and the following two are unique: (i) S6 in females broader than long (Fig. 17A); and (ii) cuspis and digitus of volsella broadly separated from each other (Fig. 29A). The monophyly of *Xanthocotelles* is relatively strongly supported by both IW (GC = 86, BS = 81) and EW (GC = 76, BS = 61) analyses, although most of its internal nodes are weakly supported overall. The clade containing *X. aisen* Toro & Cabezas, *X. basitarsis*, *X. subandina* and *X. tarsalis*, which is present in both trees, is supported by hind basitarsus with the anterior surface emarginate (Fig. 25H) and T7 covered with pale tomentum; both of these male features are unique. The relationships among the other species of the genus vary between the two analyses, except that *X. adesmiae* Toro & Cabezas and *X. fritzi* Toro & Cabezas are sister taxa in both.

The small genus *Hemicotelles* is supported by six homoplastic synapomorphies, most of which are shared with members of *Colletes*. These include S6 with a poorly-sclerotized area in the females (Fig. 17D), and dorsal wing of the penis valve with a medial spine (Fig. 32D) in the males. The monophyly of *Hemicotelles*, nonetheless, is relatively strongly supported by the EW analysis (GC = 89, BS = 84), but little less so by the IW one (GC = 74, BS = 77).

The megadiverse genus *Colletes* is supported by forewing with the second recurrent (2m-cu) vein sigmoidal in both sexes (Fig. 3D). This feature, however, is reversed to its plesiomorphic condition ‘vein only slightly arcuate outwardly’ (Fig. 3C) in *R. albicinctus*, *C. atripes* Smith and *C. perileucus* Cockerell. The genus is also supported by eight homoplastic synapomorphies. Clypeus with a pair of subapical circular pits (Fig. 6J) is uniquely exhibited by females of *Colletes*, although reversals (*i.e.* clypeus with a subapical long transverse depression; Fig. 6H) occur in *C. graffei* Alfken and *C. eous* Morice. The presence of a series of longitudinal carinae (or short striae) on the subhorizontal surface of metapostnotum (Fig. 4E) is unique among the Colletinae, even though it is homoplasiously shared with *Hylaeus modestus* Say. In the males of *Colletes*, the dorsal surface of T1 is subequal in length to that of T2 (Fig. 26D), a feature that is also exhibited by *X. basitarsis* + *X. tarsalis*. In spite of the significant number of synapomorphies, the support for *Colletes* is reasonably low (IW: GC = 75, BS = 60; EW: GC = 46, BS = 39). The relationships among the *Colletes* species differ drastically between the analyses, and in both most nodes received negative GC values and/or BS equal to zero.

## Discussion

In this study, we constructed a morphological phylogeny for the bee subfamily Colletinae with the objective of providing an updated, generic classification. Both EW and IW analyses were able to resolve the higher-level relationships among the Colletinae and permitted us to reinstate Toro and Cabezas’ (1977, 1978) classification of the group—*i.e.* containing *Colletes*, *Hemicotelles*, *Mourecozelles* and *Xanthocoelletes* each at the generic level. Overall, the four genera are relatively well-supported by the IW analysis (Fig. 35), which led us to use the resulting fittest tree to optimize the characters (Figs 36, 37). The EW analysis provided different degrees of support for each genus, lowest for *Colletes* and highest for *Hemicotelles* (Fig. 34). Nevertheless, all genera are supported by a significant number of synapomorphies which include,

at least, one unique synapomorphy (except *Hemicotelles* that is supported only by homoplastic features). A revised classification based on the results of our phylogenetic analyses appears, therefore, warranted.

The subdivision of *Mourecotelles* s.l. into three subgenera—*Mourecotelles* s.str., *Hemicotelles* and *Xanthocotelles*—as proposed by Michener (1989) is not supported by our phylogenetic results. Instead, they show that *Hemicotelles* and *Colletes* are sister taxa, meaning that the latter would render *Mourecotelles* s.l. paraphyletic. The sister-group relationship between *Hemicotelles* and *Colletes* is also corroborated by the findings of recently published molecular phylogenies of colletid bees (Almeida & Danforth, 2009; Kuhlmann *et al.*, 2009; Almeida *et al.*, 2012, 2019). Michener united the three genera under *Mourecotelles* s.l. with the justification that they share two features that are absent in *Colletes*: T1 with anterior surface concave (Fig. 26B) (as opposed to flat in *Colletes*; Fig. 26A), and with dorsal surface shorter than that of T2 (Fig. 26C) (as opposed to subequal in *Colletes*; Fig. 26D). However, both features are also exhibited by *C. cyanescens* (Haliday) and are, in fact, plesiomorphic within Colletinae.

Unlike other ground-nesting groups of bees, the Colletinae do not possess a well-developed pygidial plate, a structure that is typically used by the females in the construction of brood cells in the soil (Michener, 2007). Both *Hemicotelles* and *Xanthocotelles* have a rudimentary pygidial plate (except that it is completely absent in *X. aisen*), which is indicated by a longitudinal ridge in the former (Fig. 15B), and by either a small tubercle (Fig. 15C) or a subtriangular protrusion (Fig. 15D) in the latter. Both *Colletes* and *Mourecotelles* are completely devoid of any indication of a pygidial plate (Figs 14A–C). Interestingly, the ancestral state reconstruction suggests that the ancestral Colletinae may have had a well-developed pygidial plate, which was then convergently lost in *Colletes* and *Mourecotelles*, and drastically reduced independently in *Hemicotelles* and *Xanthocotelles*.

Both analyses show that the *Colletes* lineages of oldest divergence are all South American further supporting that the genus most likely arose on that continent, as previously suggested (Michener, 1979, 2007; Kuhlmann *et al.*, 2009; Almeida *et al.*, 2012). Among these is *C. albicinctus* from southeastern Brazil, a remarkable species the male of which possesses a series of autapomorphies, such as short mandibles, extremely elongate malar area and hind tarsomeres with long lobes directed posteriorly (Fig. 25N). Moure described *C. albicinctus* in its own genus, *Rhynchocolletes*, following a trend at the time (Cockerell, 1910; Friese, 1921;



Noskiewicz, 1936; Moure, 1943) of erecting monotypic taxa for highly autapomorphic *Colletes* species (Michener, 1989, 2007). The male also exhibits metallic bluish reflections on the metasoma, a feature that is very uncommon among the species of the genus. The presence of metasomal metallic reflections (Figs 13C; 26B,F) is a synapomorphy linking *C. albincinctus* to *C. chusmiza* Rojas & Toro and *C. cyanescens* in the EW analysis, although the IW analysis indicates that this feature may have been present in the ancestral Colletinae.

Overall, the internal relationships within each genus (not applicable to *Hemicotelles*) are weakly supported, particularly those in *Colletes*, many of which received either negative GC values or zero BS (Figs 34, 35). This is probably a consequence of the great number of homoplasies shared by the members of the genus, which is indicated by very low CIs (EW = 25.2, IW = 24.4). Furthermore, the vast majority of the apomorphies are placed on terminal branches resulting in many internal nodes being supported by few character state changes (Fig. 37). The unstable phylogenetic placement of *C. clypeonitens* Swenk (North America) is likely a third factor: while the species was recovered within the clade containing *C. atripes*, *C. gilvus* Vachal and *C. rufipes* Smith (all from South America) by the EW analysis (Fig. 34), it was placed in the most derived clade as sister to *C. kozlovi* Friese (from Asia) by the IW analysis (Fig. 35). Using the commands ‘prunnelsen’ (Goloboff *et al.*, 2008) and ‘pcrprune’ (Goloboff & Szumik, 2015) in TNT, we confirmed that *C. clypeonitens* is a rogue taxon, although additional analysis without it failed to provide significantly higher support for the clades. *Colletes clypeonitens* was nested within a South American clade in Kuhlmann *et al.*’s (2009) molecular phylogeny of the genus, which similarly to ours had weakly supported internal nodes overall.

One Neotropical subgenus (*Ptilopoda* Friese) and a series of Old World subgenera (*Rhinocolletes* Cockerell, *Denticolletes* Noskiewicz, *Pachycolletes* Bischoff, *Albocolletes* Warncke, *Elecolletes* Warncke, *Nanocolletes* Warncke, *Simcolletes* Warncke) have already been erected within *Colletes* (Cockerell, 1910; Friese, 1921; Noskiewicz, 1936; Stoeckhert, 1954; Warncke, 1978). Michener (1989) suggested that they should not be recognized until the genus was studied in a global scale, a position that he later sustained (Michener, 2007). More recently, Kuhlmann *et al.* (2009) revised the available subgenera thus making the intrageneric classification of *Colletes* phylogenetically more accurate. Given that most clades within *Colletes* in our phylogeny are weakly supported, addressing the status subgroups of the genus seems unreasonable at this time.

## ***Revised generic classification of Colletinae***

Colletinae Lepeletier de Saint-Fargeau, 1841

*Colletes* Latreille, 1802

*Mourecotelles* Toro & Cabezas, 1977

*Hemicotelles* Toro & Cabezas, 1977

*Xanthocotelles* Toro & Cabezas, 1978

### ***Colletes* Latreille, 1802**

Type species: *Apis succinctus* Linnaeus, 1758.

*Evodia* Panzer, 1806. Type species: *Apis calendarum* Panzer, 1806 (junior synonym of *Apis succincta* Linnaeus, 1758).

*Monia* Westwood, 1875 (junior homonym of *Monia* Gray, 1850). Type species: *Monia grisea* Westwood, 1875.

*Monidia* Cockerell, 1905 (new name for *Monia* Westwood (not Gray)).

*Colletes* (*Ptilopoda*) Friese, 1921. Type species: *Colletes maculipennis* Friese, 1921 (junior synonym of *Colletes spiloptera* Cockerell, 1917).

*Colletes* (*Puncticolletes*) Noskiewicz, 1936. Type species not designated thus not valid.

*Rhynchocolletes* Moure, 1943. Type species: *Rhynchocolletes albicinctus* Moure, 1943. **stat. rev.**

*Diagnosis:* Among the Colletinae, both sexes of *Colletes* can be diagnosed by the presence of a series of longitudinal carinae (or sinuous striae) on the metapostnotal subhorizontal surface (Fig. 4E) (metapostnotal subhorizontal without carinae or striae [Figs 4C,D] in the other genera). In *Colletes*, the second recurrent vein of the forewing is almost always sigmoidal (Fig. 3D), but in a few species it may be only slightly arcuate outwardly (Fig. 3C) as it is in both *Mourecotelles* and *Xanthocotelles*. The males of *Colletes* are unique among the subfamily in having T1 subequal in length to T2 (Fig. 26D) (T1 much shorter than T2 [Fig. 26C] in males of the other three genera, except *X. basitarsalis* and *X. tarsalis*). The females of *Colletes* can be further differentiated from those of *Hemicotelles* by T6 without a posteromedial longitudinal ridge (Figs 14A–C) (T6 with such a ridge [Fig. 15B] in *Hemicotelles*); and from those of both *Mourecotelles* and

*Xanthocotelles* by apical and preapical mandibular teeth forming a weak obtuse angle (Fig. 5E) (mandibular teeth forming a right angle [Fig. 5F] in *Mourecotelles* and *Xanthocotelles*).

*Additional species:* For an updated checklist refer to Ascher & Pickering (2019).

*Comments:* *Colletes* includes representatives on all continents (except Oceania), and is by far the most diverse genus of Colletinae with approximately 520 valid described species currently (Ascher & Pickering, 2019), from a suggested total estimated to be 700 (Kuhlmann *et al.*, 2009). Indeed, the large number of new species described in recent taxonomic treatments of the genus—*e.g.* Africa (Kuhlmann, 2007; Kuhlmann & Pauly, 2013; Kuhlmann & Proshchalykin, 2015), Asia (Dubitzky & Kuhlmann, 2004; Kuhlmann & Proshchalykin, 2011, 2013, 2014, 2015; Niu *et al.*, 2013, 2014; Proshchalykin & Kuhlmann, 2015), Central America (Genaro, 2001, 2003; Balboa *et al.*, 2017), Europe (Kuhlmann & Proshchalykin, 2016), North America (Neff, 2004; Hall *et al.*, 2016) and South America (Ferrari & Silveira, 2015; Ferrari, 2017, 2019b) Americas—suggest that there is still a remarkable diversity yet to be discovered. As delimited herein, *Colletes* also includes *Rhynchocolletes* as suggested previously by Michener (1989, 2007).

### ***Hemicotelles* Toro & Cabezas, 1977**

Type species: *Lonchopria ruizii* Herbst, 1923.

*Diagnosis:* Females of *Hemicotelles* are diagnosed by T6 with a posteromedial longitudinal ridge (Fig. 15B) (T6 with a posteromedial protrusion that can be either weak and rounded [Fig. 15C] or strong and subtriangular [Fig. 15D] in *Xanthocotelles*, and with no protrusion [Figs 14A–C] in both *Colletes* and *Mourecotelles*). Males of *Hemicotelles* can be differentiated from those of the other Colletinae by the following combination of characteristics: apical mandibular tooth much longer than preapical tooth (Fig. 18A); legs dark-brown to black (Figs 1A,B); and T1 much shorter than T2 (Fig. 26C) (apical tooth only slightly longer than preapical one [Fig. 18B] in *Mourecotelles*; legs pale-yellow to dark-orange [Figs 1E,F] in *Xanthocotelles*; and T1 subequal in length to T2 [Fig. 26D] in *Colletes*). *Hemicotelles* can be further distinguished from *Colletes* by forewing with second recurrent vein straight (Fig. 3B) (forewing with second recurrent vein



either sigmoidal [Fig. 3D] or slightly arcuate outwardly [Fig. 3C] in *Colletes*); and from both *Mourecotelles* and *Xanthocotelles* by metapostnotal subhorizontal and vertical surfaces separated from each other by a transverse carina broadly interrupted medially (Fig. 4D) (metapostnotum without transverse carina [Fig. 4C] in *Mourecotelles* and *Xanthocotelles*).

*Additional species:* *H. magallanes* Toro & Cabezas, 1977.

*Comments:* *Hemicotelles* is the least diverse genus of Colletinae with only two species—*H. magallanes* (southern Chile and Argentina) and *H. ruizii* (central Chile)—although there seems to be an undescribed species from southern Argentina according to unpublished morphological and barcode data.

### ***Mourecotelles* Toro & Cabezas, 1977**

Type species: *Mourecotelles mixta* Toro & Cabezas, 1977.

*Diagnosis:* Mandible with a broadly truncate preapical tooth (Fig. 5D) is sufficient to distinguish the females of *Mourecotelles* from those of the other genera of Colletinae, in which the preapical tooth is narrowly rounded (Fig. 5C). The males of the genus can be diagnosed through the combination of mandibular apical tooth only slightly longer than preapical one (Fig. 18B); and T6 marginal zone not covered with pale tomentum (mandibular apical tooth distinctly longer than preapical one [Fig. 18A] in both *Colletes* and *Hemicotelles*; and T6 marginal zone covered with tomentum in *Xanthocotelles*). *Mourecotelles* can be further differentiated from both *Colletes* and *Hemicotelles* by metapostnotum without transverse carina (Fig. 4C) (metapostnotum with transverse carina [Figs 4D,E] in *Colletes* and *Hemicotelles*); and from *Xanthocotelles* by hind tibia and basitarsus dark-brown to black (Figs 1C,D) (pale-yellow to dark-orange [Figs 1E,F] in *Xanthocotelles*).

*Additional species:* *M. boliviensis* Toro & Cabezas, 1977, *M. brevipes* (Fries, 1922), *M. chillan* Toro & Cabezas, 1977, *M. enodis* (Toro & Cabezas, 1977), *M. moldenkei* Toro & Cabezas, 1977, *M. nigripes* (Fries, 1922), *M. puelche* Toro & Cabezas, 1977, *M. rubicola* (Benoist, 1942), *M. spinolae* (Crawford & Titus, 1904), and *M. triciliatus* Toro & Cabezas, 1977.

*Comments:* Species of *Mourecotelles* are distributed primarily in Argentina and Chile (Toro & Cabezas, 1977, 1978; Michener, 1989, 2007; Moure & Urban, 2002; Moure *et al.*, 2007; Ascher & Pickering, 2019), although there is at least one species in each of Bolivia (*M. nigripes*), Ecuador (*M. rubicola*), Costa Rica (*M. brevipes*) and Brazil (*Mourecotelles* sp.). In fact, the placement of these species within *Mourecotelles* is only tentative (and follows Moure *et al.*, 2012) as they were not included in our phylogenetic analyses, except *Mourecotelles* sp. which is sister to the remaining species of the genus. One of us (RRF) has examined the male holotype of *M. triciliatus* and the species is undoubtedly a *Mourecotelles*. Neither the subgeneric division of *Mourecotelles* proposed by Michener (1989), nor its synonymy with *Rhynchocolletes* (Moure *et al.* 2007, 2012), are supported by the results of our phylogenetic analyses.

### ***Xanthocotelles* Toro & Cabezas, 1978**

Type species: *Xanthocotelles adesmiae* Toro & Cabezas, 1978.

*Diagnosis:* Females of *Xanthocotelles* are unique among the Colletinae in having S6 broader than long (Fig. 17A) (S6 longer than broad [Figs 17B–F] in the other genera of Colletinae). They can also be differentiated from the females of the other genera (except those of *Hemicotelles*) by hind tarsal claws without subapical teeth (Fig. 12I). Males of *Xanthocotelles* can be diagnosed through the combination of T1 much shorter than T2 (Fig. 26C); and T6 marginal zone covered with pale tomentum (T1 subequal to T2 in *Colletes* [Fig. 26D], and T6 marginal zone not covered with tomentum in *Hemicotelles* and *Mourecotelles*). Both sexes of *Xanthocotelles* can be further differentiated from those of *Colletes* and *Hemicotelles* by metapostnotum without transverse carina (Fig. 4C) (metapostnotum with transverse carina [Figs 4D,E] in *Colletes* and *Hemicotelles*); and from *Mourecotelles* by hind tibia and basitarsus pale-yellow to dark-orange (Figs 1E,F) (hind tibia and basitarsus dark-brown to black [Figs 1C,D] in *Mourecotelles*).

*Additional species:* *X. aisen* Toro & Cabezas, 1978, *X. andinus* (Ruiz, 1938), *X. atacama* Toro & Cabezas, 1978, *X. basitarsalis* Toro & Cabezas, 1978, *X. fritzi* Toro & Cabezas, 1978, *X. incahuasi* Toro & Cabezas, 1978, *X. plantaris* (Vachal, 1909), *X. sicheli* (Vachal, 1909), *X. subandinus* Toro & Cabezas, 1978, and *X. tarsalis* Toro & Cabezas, 1978.

*Comments:* *Xanthocotelles* is found only in Chile and Argentina. The placement of *X. plantaris* within the genus is tentative (and follows Moure & Urban, 2002; Moure *et al.*, 2007, 2012) as it was not included in our phylogenetic analyses.

***Key to the genera of Colletinae:***

1. Metapostnotal subhorizontal surface well-delimited and separated from vertical surface by a transverse carina that may be complete (Fig. 4E) or interrupted medially (Fig. 4D). Female: mandible with apical and preapical teeth forming a weak obtuse angle (Fig. 5E). Male: mandibular apical tooth distinctly longer than preapical one (Fig. 18A) ..... 2
- Metapostnotal subhorizontal surface poorly-delimited and evenly curving on to vertical surface, without transverse carina (Fig. 4C). Female: mandible with apical and preapical teeth forming an almost right angle (Fig. 5F). Male: mandibular apical tooth only slightly longer than preapical one (Fig. 18B) ..... 3
  
2. Subhorizontal surface of metapostnotum with longitudinal carinae or sinuous striae (Fig. 4E); forewing with second recurrent (2m-cu) vein sigmoidal (Fig. 3D) or, at least, with posterior part arcuate outwardly (Fig. 3C). Female: T6 without posteromedial longitudinal ridge (Figs 14A–C). Male: T1 subequal in length to T2 (Fig. 26D) ..... *Colletes* Latreille, 1802
- Subhorizontal surface of metapostnotum without longitudinal carinae or low striae (Fig. 4D); forewing with second recurrent (2m-cu) vein straight (Fig. 3B). Females: T6 with a posteromedial longitudinal ridge (Fig. 15B). Males: T1 much shorter than T2 (Fig. 26C) ..... *Hemicotelles* Toro & Cabezas, 1977
  
3. Hind tibia and basitarsus dark-brown to black (Figs 1C,D). Female: mandible with preapical tooth broadly truncate (Fig. 5D); hind tarsal claws with subapical teeth (Fig. 12J). Male: T6 marginal zone not covered with tomentum ..... *Mourecotelles* Toro & Cabezas, 1977
- Hind tibia and basitarsus pale-yellow to dark-orange (Figs 1E,F). Female: mandible with preapical tooth narrowly rounded (Fig. 5C); hind tarsal claws without subapical teeth (Fig. 12I). Male: T6 marginal zone covered with pale tomentum ..... *Xanthocotelles* Toro & Cabezas, 1978

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## Appendix I: Supplementary tables

**Table S1.** Alternative, generic classifications of Colletinae currently available. In this study, the subfamily is treated in the narrowest sense including only *Colletes* and its closest South American relatives, following Almeida & Danforth (2009).

<b>Taxon/ classification</b>	<b>Michener (1989, 2007)</b>	<b>Moure &amp; Urban (2002)</b>	<b>Moure <i>et al.</i> (2007, 2012)</b>	<b>Ascher &amp; Pickering (2019)</b>
Colletinae	includes Paracolletini <sup>1</sup> + Scrapperini <sup>2</sup>	not specified	= family Colletidae of Michener (2007)	contains only <i>Colletes</i> + <i>Mourecotelles</i>
<i>Colletes</i> Latreille, 1802	includes <i>Rhynchocolletes</i>	does not include <i>Rhynchocolletes</i>	does not include <i>Rhynchocolletes</i>	includes <i>Rhynchocolletes</i>
<i>Hemicotelles</i> Toro & Cabezas, 1977	subgenus of <i>Mourecotelles</i>	valid genus	valid genus	subgenus of <i>Mourecotelles</i>
<i>Mourecotelles</i> Toro & Cabezas, 1977	valid genus (includes <i>Hemicotelles</i> and <i>Xanthocotelles</i> as subgenera)	valid genus (not divided into subgenera)	junior synonym of <i>Rhynchocolletes</i>	valid genus (includes <i>Hemicotelles</i> and <i>Xanthocotelles</i> as subgenera)
<i>Rhynchocolletes</i> Moure, 1943	junior synonym of <i>Colletes</i>	valid genus (contains only <i>R. albicinctus</i> )	valid genus (= <i>Mourecotelles</i> of Moure & Urban [2002] + <i>R. albicinctus</i> )	junior synonym of <i>Colletes</i>
<i>Xanthocotelles</i> Toro & Cabezas, 1978	subgenus of <i>Mourecotelles</i>	valid genus	valid genus	subgenus of <i>Mourecotelles</i>

<sup>1</sup>It corresponds to the subfamily Neopasiphaeinae of Almeida *et al.* (2012) plus *Callomelitta* Smith, 1853 and *Paracolletes* Smith, 1853.

<sup>2</sup>Tribe erected by Melo & Gonçalves (2005) and later placed in its own subfamily (Scrapperinae) by Almeida & Danforth (2009). It contains only *Scrapper* Lepeletier de Saint-Fargeau & Serville, 1828.

**Table S2.** List of the species-level taxa, and their respective classification within Colletidae, included in the phylogenetic analyses of this study. Presented here also the collection data and repositories of the specimens studied. Asterisks indicate the type-species of each genus. AMNH: American Museum of Natural History; PCYU: Packer Collection at York University; UFMG: Taxonomic Collections of the Universidade Federal de Minas Gerais.

Species	Classification <sup>1</sup>	Locality	Repository
<i>Mydrosoma sabarensis</i> Silveira & Martines, 2009	Diphaglossinae	Brazil, Minas Gerais, Catas Altas	UFMG
<i>Euhesma sybilae</i> Exley, 2001	Euryglossinae	Australia, Western Australia, 5.8km N of Menzies	PCYU
<i>Xanthesma megastigma</i> (Exley, 1978)	Euryglossinae	Australia, Western Australia, Boorabin Rock National Park	PCYU
<i>Hylaeus modestus</i> Say, 1837	Hylaeinae	United States, Minnesota, Minneapolis	PCYU
<i>Hyleoides concinna</i> (Fabricius, 1775)	Hylaeinae	Australia, South Australia, Adelaide	AMNH
<i>Hexanthesa entrerriana</i> Roig-Alsina, 2006	Neopasiphaeinae	Argentina, Corrientes, Parque Nacional Mburucuya	PCYU
<i>Trichocolletes dowerinensis</i> Rayment, 1931	Neopasiphaeinae	Australia, Western Australia, Boorabin Rock National Park	PCYU
<i>Scrapter heterodoxus</i> (Cockerell, 1921)	Scrapterinae	South Africa, Western Cape, 1km N of Struisbaai	PCYU
<i>Scrapter spinipes</i> Kuhlmann, 2014	Scrapterinae	South Africa, Northern Cape, 12km NW of Nieuwoudtville	PCYU
<i>Chilicola herbsti</i> (Friese, 1906)	Xeromelissinae	Chile, Region VII, Talca	PCYU
<i>Xenochilicola diminuta</i> Toro & Moldenke, 1979	Xeromelissinae	Chile, Region III, S of Agua Dulce	PCYU
<i>Colletes albomaculatus</i> (Lucas, 1849)	Colletinae	Greece, Magnesia, Volos	PCYU
<i>Colletes americanus</i> Cresson, 1868	Colletinae	Canada, Ontario, Calendon	PCYU
<i>Colletes atripes</i> Smith, 1854	Colletinae	Chile, Region IV, Parque Nacional Fray Jorge	PCYU
<i>Colletes bombiformis</i> Metz, 1910	Colletinae	Guatemala, Sacatepéquez, Antigua Guatemala	PCYU
<i>Colletes capensis</i> Cameron, 1905	Colletinae	South Africa, Western Cape, Wiedouw River	PCYU
<i>Colletes chusmiza</i> Rojas & Toro, 1993	Colletinae	Chile, Region I, Chusmiza	PCYU
<i>Colletes clypeonitens</i> Swenk, 1906	Colletinae	United States, California, San Bernadino	PCYU
<i>Colletes compactus</i> Cresson, 1868	Colletinae	Canada, Ontario, Forks of Credit Provincial Park	PCYU
<i>Colletes coriandri</i> Pérez, 1895	Colletinae	Egypt, Sinai, Wadi Rum	PCYU
<i>Colletes cyanescens</i> (Haliday, 1836)	Colletinae	Argentina, Santa Cruz, Los Antiguos	PCYU
<i>Colletes eous</i> Morice, 1904	Colletinae	Greece, Magnesia, Volos	PCYU
<i>Colletes eulophi</i> Robertson, 1891	Colletinae	United States, Utah, Kane County	PCYU
<i>Colletes gilvus</i> Vachal, 1909	Colletinae	Peru, Ica, 39km E of Nazca	PCYU
<i>Colletes graeffei</i> Alfken, 1900	Colletinae	Italy, Lombardia, 20km NE of Brescia	PCYU
<i>Colletes hirtibasis</i> Cockerell, 1936	Colletinae	South Africa, East Cape, Studispoort Bavianskloof	PCYU
<i>Colletes hyalinus</i> Provancher, 1888	Colletinae	Canada, Yukon, 17km WNW of Fort Selkirk	PCYU
<i>Colletes impunctatus</i> Nylander, 1852	Colletinae	Mongolia, Khövsgöl, 22km ENE of Khatgal	PCYU

<i>Colletes inaequalis</i> Say, 1837	Colletinae	Canada, Ontario, Muskoka	PCYU
<i>Colletes inexpectatus</i> Noskiewicz, 1936	Colletinae	Tajikistan, Gorno-Badakhshan, Khorugh	PCYU
<i>Colletes kozlovi</i> Friese, 1914	Colletinae	Mongolia, Dornogovi, 70km of Saynshand	PCYU
<i>Colletes lacunatus</i> Dours, 1872	Colletinae	Egypt, Ismailia, Ismaila	PCYU
<i>Colletes nasutus</i> Smith, 1853	Colletinae	Slovakia, Nitra, Marcelová	PCYU
<i>Colletes nigrifrons</i> Titus, 1900	Colletinae	Canada, Yukon, 3.5km NE of Fort Selkirk	PCYU
<i>Colletes nigrutilus</i> Friese, 1910	Colletinae	Argentina, Chubut, INTA Trevelin	PCYU
<i>Colletes perileucus</i> Cockerell, 1924	Colletinae	Mexico, Sonora, 30km E of Agua Prieta	PCYU
<i>Colletes petropolitanus</i> Dalla Torre, 1896	Colletinae	Paraguay, San Pedro, Cororo	PCYU
<i>Colletes rufipes</i> Smith, 1879	Colletinae	Brazil, Minas Gerais, Nova Lima	UFMG
<i>Colletes simulans</i> Cresson, 1868	Colletinae	Canada, Ontario, Caledon	PCYU
<i>Colletes succinctus</i> (Latreille, 1758)*	Colletinae	Germany, Lower Saxony, Auf der Horst	PCYU
<i>Hemicotelles magallanes</i> Toro & Cabezas, 1977	Colletinae	Argentina, Santa Cruz, 8km S of Los Antiguos	PCYU
<i>Hemicotelles ruizii</i> (Herbst, 1923)*	Colletinae	Chile, Region IV, Vicuña	AMNH
<i>Mourecotelles boliviensis</i> Toro & Cabezas, 1977	Colletinae	Argentina, Jujuy, Abra Pampa	AMNH
<i>Mourecotelles chillan</i> Toro & Cabezas, 1977	Colletinae	Chile, Region VIII, Chillán	AMNH
<i>Mourecotelles enodis</i> (Vachal, 1909)	Colletinae	Chile, Region VII, Curicó	AMNH
<i>Mourecotelles mixtus</i> Toro & Cabezas, 1977*	Colletinae	Chile, Region IV, 1.1km S of Tololo Observatory	PCYU
<i>Mourecotelles moldenkei</i> Toro & Cabezas, 1977	Colletinae	Argentina, Santa Cruz, 8km S of Los Antiguos	PCYU
<i>Mourecotelles puelche</i> Toro & Cabezas, 1977	Colletinae	Chile, Metropolitan Region, Farellones	AMNH
<i>Mourecotelles</i> sp.	Colletinae	Brazil, Paraná, Guarapuava	PCYU
<i>Mourecotelles spinolae</i> (Crawford & Titus, 1904)	Colletinae	Argentina, Salta, Cuesta Obispo	AMNH
<i>Rhynchocolletes albicinctus</i> Moure, 1943*	Colletinae	Brazil, Santa Catarina, Nova Teutônia	AMNH
<i>Xanthocolletes adesmiae</i> Toro & Cabezas, 1978*	Colletinae	Chile, Region V, Colliguay	PCYU
<i>Xanthocolletes aisen</i> Toro & Cabezas, 1978	Colletinae	Chile, Region XII, Laguna Azul	AMNH
<i>Xanthocolletes andinus</i> (Ruiz, 1938)	Colletinae	Chile, Region IV, Laguna Verde	AMNH
<i>Xanthocolletes atacama</i> Toro & Cabezas, 1978	Colletinae	Chile, Region III, Quebrada del Potrero	PCYU
<i>Xanthocolletes basitarsis</i> Toro & Cabezas, 1978	Colletinae	Argentina, San Juan, Río Agua Negra	AMNH
<i>Xanthocolletes fritzi</i> Toro & Cabezas, 1978	Colletinae	Chile, Region VIII, Melipilla	AMNH
<i>Xanthocolletes incahuasi</i> Toro & Cabezas, 1978	Colletinae	Chile, Region IV, 6km S of Vicuña	PCYU
<i>Xanthocolletes sicheli</i> (Vachal, 1909)	Colletinae	Chile, Region VIII, Chillán	AMNH
<i>Xanthocolletes subandinus</i> Toro & Cabezas, 1978	Colletinae	Chile, Valparaíso, Guardia Vieja	AMNH
<i>Xanthocolletes tarsalis</i> Toro & Cabezas, 1978	Colletinae	Argentina, Jujuy, Tres Cruces	AMNH

<sup>1</sup>Subfamilies of Colletidae recognized by Almeida *et al.* (2012, 2019).

**Table S3.** Discrete character matrix for the species included in the phylogenetic analyses. -: inapplicable, question mark: missing data.

Species	Characters																											
	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
<i>Mydrosoma sabarensis</i>	0	0	0	0	-	-	?	1	0	0	-	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	-
<i>Euhesma sybilae</i>	0	?	?	0	-	-	2	1	0	0	-	0	0	0	-	1	0	0	0	0	0	1	0	0	0	0	-	
<i>Xanthesma megastigma</i>	0	?	?	0	-	-	0	1	0	0	-	0	0	0	-	1	0	0	0	0	0	0	0	?	0	0	-	
<i>Hylaeus modestus</i>	0	0	0	1	2	0	0	0	-	0	-	0	0	0	-	1	0	0	1	0	0	0	0	?	0	0	-	
<i>Hyleoides concinna</i>	1	0	0	?	?	?	0	0	-	1	1	0	0	0	-	1	0	0	1	0	0	0	0	0	0	0	-	
<i>Hexanthesa entrerriana</i>	0	0	0	0	-	-	0	1	0	0	-	1	0	1	0	2	0	0	0	-	0	0	0	0	0	0	-	
<i>Trichocolletes dowerinensis</i>	0	0	0	0	-	-	0	1	0	0	-	1	0	1	0	2	0	0	0	-	0	0	0	0	0	0	-	
<i>Scrapter heterodoxus</i>	0	0	0	0	-	-	0	1	0	0	-	0	1	0	-	1	0	0	0	0	0	1	0	0	0	0	-	
<i>Scrapter spinipes</i>	0	0	0	0	-	-	0	1	0	0	-	0	0	0	-	1	0	0	0	0	0	0	0	0	0	0	-	
<i>Chilicola herbsti</i>	0	0	0	0	-	-	1	1	0	0	-	0	0	0	-	1	0	0	0	-	0	0	0	0	0	0	-	
<i>Xenochilicola diminuta</i>	0	0	0	0	-	-	0	1	1	0	-	0	0	1	1	0	1	0	0	-	0	0	0	?	0	0	-	
<i>Colletes albomaculatus</i>	0	0	0	1	2	1	0	1	1	0	-	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	
<i>Colletes americanus</i>	0	0	0	0	-	-	0	1	2	0	-	1	0	1	0	1	0	0	0	0	-	1	0	0	0	0	-	
<i>Colletes atripes</i>	0	0	0	0	-	-	2	1	2	0	-	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	
<i>Colletes bombiformis</i>	0	0	0	1	2	0	2	1	2	0	-	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	
<i>Colletes capensis</i>	0	0	0	1	2	1	2	1	2	0	-	1	0	1	1	1	1	0	0	0	1	0	0	0	0	0	-	
<i>Colletes chusmiza</i>	0	0	0	0	-	-	1	1	2	0	-	0	2	1	1	0	0	0	0	0	1	0	0	0	0	0	0	
<i>Colletes clypeonitens</i>	0	0	0	1	1	-	0	1	2	0	-	1	0	1	1	0	0	0	0	1	1	0	1	0	0	1	1	
<i>Colletes compactus</i>	0	0	0	1	2	0	2	1	2	0	-	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	-	
<i>Colletes coriandri</i>	0	0	0	1	2	1	2	1	2	0	-	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	-	
<i>Colletes cyanescens</i>	0	0	0	1	2	1	1	1	2	0	-	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	-	
<i>Colletes eous</i>	0	0	0	1	2	1	0	1	0	0	-	1	1	1	0	1	2	1	0	0	1	0	1	0	0	1	0	
<i>Colletes eulophi</i>	0	0	0	0	-	-	0	1	2	0	-	1	0	1	0	1	1	0	0	0	0	0	1	0	0	1	0	
<i>Colletes gilvus</i>	0	0	0	1	2	1	0	1	2	0	-	1	1	1	1	0	0	0	0	0	1	0	1	0	0	1	0	
<i>Colletes graeffei</i>	0	0	0	1	2	1	0	1	2	0	-	1	0	1	0	1	0	1	0	1	-	1	1	0	0	0	-	
<i>Colletes hirtibasis</i>	0	0	0	1	2	1	2	1	2	0	-	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	-	
<i>Colletes hyalinus</i>	0	0	0	0	-	-	0	1	2	0	-	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	-	
<i>Colletes impunctatus</i>	0	0	0	0	-	-	0	1	2	0	-	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	
<i>Colletes inaequalis</i>	0	0	0	1	2	1	2	1	2	0	-	1	0	1	0	1	1	1	0	0	-	1	1	0	0	0	-	
<i>Colletes inexpectatus</i>	0	0	0	1	2	1	2	1	2	0	-	1	0	1	0	1	0	0	0	1	-	1	1	1	0	1	1	



Species	Characters																											
	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	
	0	1	2	3	4	5	6	7	8	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	
<i>Colletes kozlovi</i>	0	0	0	1	2	1	2	1	2	0	-	1	1	1	1	0	0	0	0	0	0	0	1	0	0	1	1	
<i>Colletes lacunatus</i>	0	0	0	1	2	1	0	1	2	0	-	1	0	1	1	1	1	0	0	0	0	0	0	1	0	1	0	
<i>Colletes nasutus</i>	0	0	0	1	2	1	0	1	2	0	-	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	-	
<i>Colletes nigrifrons</i>	0	0	0	1	1	1	2	1	2	0	-	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	
<i>Colletes nigrutilus</i>	0	0	0	1	2	1	2	1	2	0	-	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	
<i>Colletes perileucus</i>	0	0	0	1	2	1	2	1	2	0	-	1	0	1	0	0	0	0	0	0	-	1	1	0	1	0	-	
<i>Colletes petropolitanus</i>	0	0	0	0	-	-	0	1	2	1	0	1	1	1	1	1	0	0	0	1	1	0	1	0	0	1	0	
<i>Colletes rufipes</i>	0	0	0	1	2	1	0	1	2	0	-	1	0	1	0	1	1	0	0	0	0	0	1	0	0	0	-	
<i>Colletes simulans</i>	0	0	0	1	2	0	0	1	0	0	-	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	-	
<i>Colletes succinctus</i>	0	0	0	1	2	1	0	1	0	0	-	1	0	1	0	0	2	0	0	0	0	0	0	0	0	1	0	
<i>Hemicotelles magallanes</i>	0	0	0	1	2	1	1	1	0	0	-	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	
<i>Hemicotelles ruizii</i>	0	0	0	1	2	0	1	1	0	0	-	0	1	1	1	0	0	0	0	0	0	0	1	0	0	1	1	
<i>Mourecotelles boliviensis</i>	0	1	1	1	0	-	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	
<i>Mourecotelles chillan</i>	0	1	1	1	0	-	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	
<i>Mourecotelles enodis</i>	0	1	1	1	0	-	1	1	1	1	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	
<i>Mourecotelles mixtus</i>	0	1	1	1	0	-	1	1	1	1	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1	
<i>Mourecotelles mondelkei</i>	0	1	1	1	0	-	1	1	1	1	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1	
<i>Mourecotelles puelche</i>	0	1	1	1	0	-	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	
<i>Mourecotelles sp.</i>	0	1	1	1	0	-	0	1	1	1	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1	
<i>Mourecotelles spinolae</i>	0	1	1	1	0	-	0	1	1	0	-	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	
<i>Rhynchocolletes albicinctus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Xanthocotelles adesmiae</i>	0	0	1	1	2	0	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	
<i>Xanthocotelles aisen</i>	0	0	1	1	2	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	
<i>Xanthocotelles andinus</i>	0	0	1	1	2	0	1	1	1	1	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1	
<i>Xanthocotelles atacama</i>	0	0	1	1	2	0	1	1	1	0	-	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1	
<i>Xanthocotelles basitarsis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	
<i>Xanthocotelles fritzi</i>	0	0	1	0	-	-	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	
<i>Xanthocotelles incahuasi</i>	0	0	1	1	2	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	
<i>Xanthocotelles sicheli</i>	0	0	1	1	1	-	1	1	0	0	-	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	
<i>Xanthocotelles subandinus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	
<i>Xanthocotelles tarsalis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	

Species	Characters																											
	2	2	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5
	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
<i>Mydrosoma sabarensis</i>	1	1	0	0	1	0	0	0	1	1	0	0	1	1	0	1	0	0	-	0	-	0	0	0	0	-	0	0
<i>Euhesma sybilae</i>	1	0	2	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	-	1	1	0	1	0	0	-	1	1
<i>Xanthesma megastigma</i>	0	0	2	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	-	1	1	0	1	0	0	-	1	1
<i>Hylaeus modestus</i>	0	0	0	0	1	0	0	0	0	0	-	0	0	0	1	1	0	0	-	0	-	0	0	0	0	-	2	2
<i>Hyleoides concinna</i>	0	0	0	0	1	0	0	0	0	0	-	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	2
<i>Hexanthesa entrerriana</i>	0	1	1	0	1	0	0	0	1	1	0	0	1	2	0	1	0	1	0	0	-	0	0	0	0	-	0	0
<i>Trichocolletes dowerinensis</i>	0	1	1	1	0	0	0	0	1	1	0	0	1	1	0	1	0	1	0	0	-	0	0	0	0	-	0	0
<i>Scrapter heterodoxus</i>	0	1	0	0	0	0	0	0	1	?	?	?	?	2	0	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Scrapter spinipes</i>	0	1	0	0	0	0	0	0	1	1	0	0	0	2	0	1	0	0	-	0	-	0	1	0	0	-	1	1
<i>Chilicola herbsti</i>	0	1	0	0	1	0	0	0	0	0	-	1	0	2	1	1	0	0	-	0	-	0	1	0	0	-	1	1
<i>Xenochilicola diminuta</i>	0	0	0	0	1	0	0	0	0	0	-	1	0	2	1	1	0	0	-	0	-	0	1	0	0	-	1	1
<i>Colletes albomaculatus</i>	2	1	1	1	1	0	0	0	0	0	-	0	1	0	0	1	0	0	-	0	-	0	0	1	0	-	1	1
<i>Colletes americanus</i>	2	1	1	0	1	0	0	0	0	0	-	0	1	2	0	1	0	0	-	0	-	0	0	0	0	-	1	1
<i>Colletes atripes</i>	2	1	1	0	1	0	0	0	0	0	-	0	1	2	0	1	0	1	0	0	-	0	0	0	0	-	1	1
<i>Colletes bombiformis</i>	1	1	0	0	1	0	0	0	0	0	-	1	1	2	0	1	0	0	-	0	-	0	0	0	0	-	1	1
<i>Colletes capensis</i>	0	1	0	0	1	0	1	0	0	0	-	1	1	1	0	1	0	0	-	0	-	0	0	0	0	-	1	1
<i>Colletes chusmiza</i>	0	1	0	0	1	0	0	0	0	0	-	0	1	2	0	1	0	0	-	0	-	0	0	1	0	-	1	1
<i>Colletes clypeonitens</i>	2	1	0	0	1	1	1	1	0	0	-	0	1	1	0	1	0	1	2	0	-	0	0	0	0	-	1	1
<i>Colletes compactus</i>	0	1	0	0	1	0	1	0	0	0	-	1	1	1	0	1	1	1	2	0	-	0	0	0	1	1	1	1
<i>Colletes coriandri</i>	1	1	0	0	1	0	1	0	0	0	-	1	0	1	0	1	0	1	2	0	-	0	0	0	0	-	1	1
<i>Colletes cyanescens</i>	0	1	0	0	1	0	0	1	0	0	-	0	2	2	0	1	0	0	-	0	-	1	0	1	0	-	1	1
<i>Colletes eous</i>	1	1	0	1	1	0	1	0	0	0	-	0	1	1	0	1	0	1	0	0	-	0	0	0	0	-	1	1
<i>Colletes eulophi</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	1	0	1	0	1	2	1	1	0	0	0	0	-	1	1
<i>Colletes gilvus</i>	0	1	0	0	1	1	1	1	0	0	-	0	1	1	0	1	0	1	0	0	-	0	1	0	0	-	1	1
<i>Colletes graeffei</i>	2	1	1	0	1	0	1	0	0	0	-	0	1	1	0	1	0	1	0	0	-	0	0	0	0	-	1	1
<i>Colletes hirtibasis</i>	1	1	0	1	1	0	0	0	0	0	-	1	1	2	0	1	0	1	1	0	-	0	0	0	0	-	1	1
<i>Colletes hyalinus</i>	1	1	0	0	1	0	0	0	0	0	-	1	2	1	0	1	0	0	-	0	-	0	0	0	0	-	1	1
<i>Colletes impunctatus</i>	0	1	0	0	1	0	0	0	0	0	-	1	1	2	0	1	0	1	0	0	-	0	0	0	1	0	1	1
<i>Colletes inaequalis</i>	0	1	0	0	1	0	1	0	0	0	-	0	1	1	0	1	0	1	0	0	-	0	0	0	0	-	1	1
<i>Colletes inexpectatus</i>	0	1	1	0	1	1	1	1	0	0	-	0	1	1	0	1	0	0	-	0	-	0	0	0	0	-	1	1
<i>Colletes kozlovi</i>	0	1	0	0	1	1	1	0	0	0	-	1	1	2	0	1	0	1	0	0	-	0	0	0	1	0	1	1
<i>Colletes lacunatus</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	0

Species	Characters																											
	2	2	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	
	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	
<i>Colletes nasutus</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Colletes nigrifrons</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Colletes nigrutilus</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Colletes perileucus</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Colletes petropolitanus</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Colletes rufipes</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Colletes simulans</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Colletes succinctus</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Hemicotelles magallanes</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Hemicotelles ruizii</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Mourecotelles boliviensis</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Mourecotelles chillan</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Mourecotelles enodis</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Mourecotelles mixtus</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Mourecotelles mondolkei</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Mourecotelles puelche</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Mourecotelles</i> sp.	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Mourecotelles spinolae</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Rhynchocolletes albicinctus</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Xanthocolletes adesmiae</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Xanthocolletes aisen</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Xanthocolletes andinus</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Xanthocolletes atacama</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Xanthocolletes basitarsis</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Xanthocolletes fritzi</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Xanthocolletes incahuasi</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Xanthocolletes sicheli</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Xanthocolletes subandinus</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	
<i>Xanthocolletes tarsalis</i>	1	1	0	0	1	0	1	0	0	0	-	1	1	0	0	1	0	0	-	0	-	0	0	1	0	-	0	

Species	Characters																										
	5	5	5	5	5	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	8	8		
	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
<i>Mydrosoma sabarensis</i>	0	2	0	1	1	0	1	1	0	-	1	2	0	1	0	1	1	0	1	0	-	1	0	1	0	1	1
<i>Euhesma sybilae</i>	1	2	0	1	1	0	0	1	0	-	0	0	0	1	1	1	1	0	0	0	-	2	0	0	0	1	0
<i>Xanthesma megastigma</i>	1	2	0	1	1	0	1	0	0	-	0	2	0	1	1	1	1	0	0	0	-	2	0	0	0	1	0
<i>Hylaeus modestus</i>	1	0	0	0	0	1	1	0	0	-	0	0	0	1	1	0	-	0	0	0	-	0	0	0	0	0	2
<i>Hyleoides concinna</i>	1	0	0	1	0	1	1	0	0	-	0	0	0	1	1	0	-	0	0	0	-	0	0	1	0	1	2
<i>Hexanthesa entrerriana</i>	0	0	0	1	1	0	0	1	0	-	0	0	1	0	-	1	1	0	1	0	-	1	0	0	0	1	0
<i>Trichocolletes dowerinensis</i>	0	2	0	1	1	0	1	1	0	-	1	0	1	0	-	1	1	0	1	0	-	1	0	1	0	1	0
<i>Scrapter heterodoxus</i>	1	0	0	1	1	0	0	2	0	-	0	0	0	1	2	1	0	0	1	0	-	0	0	1	0	0	1
<i>Scrapter spinipes</i>	1	0	0	1	1	0	0	1	0	-	0	0	1	1	1	1	0	0	0	0	-	0	0	0	0	1	2
<i>Chilicola herbsti</i>	1	0	0	1	0	1	0	1	0	-	0	0	1	0	-	0	-	0	0	0	-	0	0	0	0	1	1
<i>Xenochilicola diminuta</i>	1	2	0	1	0	1	1	1	0	-	0	2	1	0	-	0	-	0	0	0	-	2	0	0	0	0	1
<i>Colletes albomaculatus</i>	0	0	0	1	0	0	0	2	0	-	0	0	0	1	2	1	0	1	1	0	-	0	0	1	0	1	3
<i>Colletes americanus</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	1	1	0	-	2	0	1	0	1	2
<i>Colletes atripes</i>	0	0	1	1	1	0	0	1	1	1	0	0	1	1	2	0	-	1	1	0	-	2	0	3	0	1	2
<i>Colletes bombiformis</i>	0	0	0	1	1	0	0	2	1	1	0	0	1	1	2	0	-	1	1	1	1	0	0	4	0	1	1
<i>Colletes capensis</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	0	1	0	-	0	0	1	0	1	2
<i>Colletes chusmiza</i>	0	0	0	1	1	0	0	0	1	1	0	2	1	1	2	0	-	0	1	1	0	0	0	4	0	1	2
<i>Colletes clypeonitens</i>	0	0	1	1	1	0	0	1	0	-	0	1	1	1	2	0	-	0	1	0	-	2	0	0	0	1	1
<i>Colletes compactus</i>	0	0	0	1	1	0	0	0	1	1	0	0	1	1	2	0	-	1	1	1	1	0	0	2	0	1	2
<i>Colletes coriandri</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	0	1	0	-	1	0	1	0	1	1
<i>Colletes cyanescens</i>	0	0	0	1	1	0	0	0	1	1	0	0	0	1	2	0	-	0	1	0	-	0	0	5	0	1	1
<i>Colletes eous</i>	0	0	0	1	1	0	0	2	0	-	0	0	0	1	2	0	-	1	1	0	-	0	0	2	0	0	3
<i>Colletes eulophi</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	2	1	0	-	2	0	1	0	1	2
<i>Colletes gilvus</i>	0	0	1	1	1	0	0	0	1	1	0	0	1	1	2	0	-	1	1	1	1	0	0	5	0	1	2
<i>Colletes graeffei</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	0	1	0	-	1	0	1	0	1	2
<i>Colletes hirtibasis</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	1	1	0	-	0	0	0	0	1	1
<i>Colletes hyalinus</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	1	1	0	-	2	0	0	0	1	2
<i>Colletes impunctatus</i>	0	0	0	1	1	0	0	2	1	0	0	0	1	1	2	0	-	0	1	0	-	1	0	2	0	1	1
<i>Colletes inaequalis</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	2	1	0	-	1	0	1	0	1	2
<i>Colletes inexpectatus</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	0	1	0	-	1	0	1	0	1	1
<i>Colletes kozlovi</i>	0	0	0	1	1	0	0	1	0	-	0	0	1	1	2	0	-	1	1	0	-	2	0	1	0	1	1
<i>Colletes lacunatus</i>	0	0	0	1	1	0	0	1	0	-	0	0	1	1	2	1	0	1	1	0	-	0	1	1	0	0	3



Species	Characters																											
	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	8	8	
	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	
<i>Colletes nasutus</i>	0	0	0	1	1	0	0	2	0	-	0	1	1	1	2	0	-	1	1	0	-	0	0	0	0	1	1	
<i>Colletes nigrifrons</i>	0	0	0	1	1	0	0	0	1	1	0	0	0	1	2	0	-	1	1	1	1	0	0	5	0	1	2	
<i>Colletes nigrutilus</i>	0	0	0	1	0	0	0	2	0	-	0	0	1	1	2	0	-	1	1	1	1	0	0	2	0	1	3	
<i>Colletes perileucus</i>	0	0	0	1	1	0	0	2	1	0	0	0	1	1	2	0	-	1	1	0	-	1	0	2	0	1	2	
<i>Colletes petropolitanus</i>	0	1	0	1	1	0	0	0	1	1	0	2	1	1	2	0	-	1	1	0	-	2	0	3	0	1	1	
<i>Colletes rufipes</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	3	1	1	1	0	0	2	0	1	2	
<i>Colletes simulans</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	0	1	0	-	1	0	1	0	1	2	
<i>Colletes succinctus</i>	0	0	0	1	1	0	0	2	0	-	0	0	1	1	2	0	-	1	1	?	?	0	0	0	1	0	3	
<i>Hemicotelles magallanes</i>	0	0	0	1	0	0	0	0	1	1	0	0	1	1	2	1	0	0	1	0	-	2	0	1	0	1	1	
<i>Hemicotelles ruizii</i>	0	0	0	1	0	0	0	0	1	1	0	0	1	1	2	1	0	0	1	0	-	2	0	3	0	1	1	
<i>Mourecotelles boliviensis</i>	0	0	1	0	0	0	0	0	1	1	0	0	0	1	2	1	1	0	1	1	0	1	0	2	0	1	1	
<i>Mourecotelles chillan</i>	0	0	1	0	0	0	0	0	1	1	0	0	0	1	2	1	1	0	1	0	-	0	0	1	0	1	1	
<i>Mourecotelles enodis</i>	0	0	1	0	0	0	0	0	1	1	0	0	0	1	2	1	1	0	1	1	0	1	0	2	0	1	1	
<i>Mourecotelles mixtus</i>	0	0	1	0	0	0	0	0	1	1	0	0	0	1	2	1	1	0	1	1	0	1	0	1	0	1	1	
<i>Mourecotelles mondolkei</i>	0	0	1	0	0	0	0	0	1	1	0	1	0	1	2	1	1	0	1	0	-	1	0	1	0	1	1	
<i>Mourecotelles puelche</i>	0	0	1	0	0	0	0	0	1	1	0	0	0	1	2	1	1	0	1	1	0	1	0	1	0	1	1	
<i>Mourecotelles</i> sp.	0	0	1	0	0	0	0	0	1	1	0	1	0	1	2	1	0	0	1	1	0	1	0	1	0	1	1	
<i>Mourecotelles spinolae</i>	0	0	0	0	0	0	0	0	1	1	0	0	0	1	2	1	1	0	1	0	-	2	0	3	0	1	1	
<i>Rhynchocolletes albicinctus</i>	0	0	1	0	0	1	0	1	1	1	0	0	1	1	2	0	-	0	1	1	1	0	0	4	0	1	1	
<i>Xanthocolletes adesmiae</i>	0	0	0	1	0	0	0	0	1	1	0	0	0	1	2	1	0	0	1	0	-	1	0	3	0	1	1	
<i>Xanthocolletes aisen</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	1	2	1	0	0	1	0	-	2	0	1	0	1	1	
<i>Xanthocolletes andinus</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	1	2	1	0	0	1	0	-	2	0	1	0	1	1	
<i>Xanthocolletes atacama</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	1	2	1	0	0	1	0	-	2	0	1	0	1	1	
<i>Xanthocolletes basitarsis</i>	0	0	0	0	0	0	0	0	1	1	0	0	0	1	2	1	0	0	1	1	0	1	0	2	0	1	1	
<i>Xanthocolletes fritzi</i>	0	0	0	1	0	0	0	0	1	1	0	0	0	1	2	1	0	0	1	0	-	1	0	2	0	1	1	
<i>Xanthocolletes incahuasi</i>	0	0	0	1	0	0	0	0	1	0	0	0	0	1	2	1	0	0	1	0	-	1	0	1	0	1	1	
<i>Xanthocolletes sicheli</i>	0	0	0	0	0	0	0	0	0	-	0	1	0	1	2	1	1	0	1	0	-	2	0	1	0	1	1	
<i>Xanthocolletes subandinus</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	1	2	1	0	0	1	0	-	1	0	1	0	1	1	
<i>Xanthocolletes tarsalis</i>	0	0	0	0	0	0	0	0	1	0	0	0	1	1	2	1	0	0	1	0	-	1	0	1	0	1	1	

Species	Characters																											
	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	9	9	1	1	1	1	1	1	1	1	1	1
	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	0	0	0	0	0	0	0	0	0
																			0	1	2	3	4	5	6	7	8	
<i>Mydrosoma sabarensis</i>	1	1	1	0	0	-	0	-	0	-	1	1	1	1	0	0	1	0	0	0	0	0	0	-	1	0	-	
<i>Euhesma sybilae</i>	0	1	1	0	0	-	1	0	0	-	0	1	0	0	0	0	1	0	1	0	0	0	0	-	1	1	0	
<i>Xanthesma megastigma</i>	0	1	1	0	0	-	1	0	0	-	0	1	0	0	0	0	1	0	1	0	0	0	0	-	1	1	0	
<i>Hylaeus modestus</i>	2	1	3	0	1	0	1	1	0	-	2	1	2	0	0	1	1	0	0	0	0	0	0	-	0	0	-	
<i>Hyleoides concinna</i>	2	1	1	0	1	0	1	0	0	-	2	1	2	0	1	1	0	0	0	0	1	0	1	2	0	0	-	
<i>Hexanthesa entrerriana</i>	1	1	1	0	0	-	1	0	0	-	0	1	0	0	1	1	0	0	1	0	2	0	0	-	1	1	0	
<i>Trichocolletes dowerinensis</i>	1	1	1	0	0	-	0	-	0	-	0	1	0	1	0	0	1	1	1	0	0	0	0	-	1	1	0	
<i>Scrapter heterodoxus</i>	2	2	2	0	1	0	0	-	0	-	1	0	0	0	0	1	1	0	1	1	0	1	0	-	1	1	0	
<i>Scrapter spinipes</i>	2	2	2	0	1	0	1	0	0	-	1	2	0	0	0	1	1	0	1	1	0	1	0	-	0	1	0	
<i>Chilicola herbsti</i>	2	1	2	0	1	0	1	0	0	-	0	2	0	0	0	1	1	0	0	0	0	0	0	-	0	0	-	
<i>Xenochilicola diminuta</i>	2	1	2	0	1	0	1	0	0	-	0	2	0	0	0	1	1	0	0	0	0	0	0	-	0	1	0	
<i>Colletes albomaculatus</i>	2	0	4	0	1	1	1	1	1	1	2	3	2	1	2	0	0	0	0	0	1	0	1	2	0	1	1	
<i>Colletes americanus</i>	2	0	3	1	1	1	1	1	1	1	1	3	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	
<i>Colletes atripes</i>	2	0	2	0	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	-	0	1	1	
<i>Colletes bombiformis</i>	1	0	3	0	1	0	1	1	1	1	1	3	2	1	2	0	0	0	0	0	2	0	0	-	0	1	1	
<i>Colletes capensis</i>	3	0	3	0	1	1	1	1	1	1	1	3	0	1	2	0	0	0	0	0	0	0	0	-	0	1	1	
<i>Colletes chusmiza</i>	2	1	1	0	1	1	1	1	1	1	1	0	0	1	2	0	0	0	0	0	0	0	1	3	0	1	1	
<i>Colletes clypeonitens</i>	1	0	2	0	1	0	1	1	1	1	1	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	0	
<i>Colletes compactus</i>	2	0	3	0	1	1	1	1	1	1	2	3	0	1	2	0	0	0	0	0	1	0	1	2	0	1	1	
<i>Colletes coriandri</i>	2	2	2	0	1	1	1	1	1	1	1	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	
<i>Colletes cyanescens</i>	1	1	1	0	1	0	1	1	1	1	1	0	0	1	2	0	0	0	0	0	0	0	1	2	1	1	0	
<i>Colletes eous</i>	3	0	4	0	1	1	1	1	1	1	2	3	0	1	2	0	0	0	0	0	0	0	0	-	0	1	1	
<i>Colletes eulophi</i>	2	0	3	0	1	1	1	1	1	1	1	2	0	1	2	0	0	0	0	0	0	0	0	-	0	1	1	
<i>Colletes gilvus</i>	1	0	3	0	1	0	1	1	1	1	1	2	0	1	2	0	0	0	0	0	0	0	1	1	0	1	1	
<i>Colletes graeffei</i>	2	0	3	0	1	1	1	1	1	1	1	2	0	1	2	0	0	0	0	0	0	0	0	-	0	1	1	
<i>Colletes hirtibasis</i>	1	0	3	0	1	1	1	1	1	1	1	3	0	1	1	0	0	0	0	0	2	0	1	0	0	1	1	
<i>Colletes hyalinus</i>	2	0	2	0	1	1	1	1	1	1	1	3	0	1	2	0	0	0	0	0	0	0	1	0	0	1	0	
<i>Colletes impunctatus</i>	2	1	2	0	1	1	1	1	1	1	1	0	0	1	2	0	0	0	0	0	1	0	1	0	0	1	1	
<i>Colletes inaequalis</i>	2	0	3	0	1	1	1	1	1	1	1	2	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	
<i>Colletes inexpectatus</i>	2	0	3	0	1	1	1	1	1	1	1	1	0	1	2	0	0	0	0	0	0	0	1	2	0	1	1	
<i>Colletes kozlovi</i>	2	1	3	0	1	1	1	1	1	1	1	0	0	1	2	0	0	0	0	0	0	0	0	-	0	1	1	

Species	Characters																											
	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	9	9	9	1	1	1	1	1	1	1	1	1
	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	0	0	0	0	0	0	0	0	0
																			0	1	2	3	4	5	6	7	8	
<i>Colletes lacunatus</i>	3	0	4	0	1	1	1	1	1	1	2	3	0	1	2	0	0	0	0	0	1	0	0	-	0	1	1	
<i>Colletes nasutus</i>	2	0	3	0	1	1	1	1	1	1	1	2	0	1	2	0	0	0	0	0	1	0	1	0	0	1	1	
<i>Colletes nigrifrons</i>	1	0	3	0	1	1	1	1	1	1	1	1	0	1	2	1	0	0	0	0	2	0	0	-	0	1	1	
<i>Colletes nigrutilus</i>	2	0	2	0	1	1	1	1	1	1	2	0	0	1	1	0	0	0	0	0	0	0	0	-	0	1	1	
<i>Colletes perileucus</i>	1	0	3	0	1	1	1	1	1	1	1	2	0	1	2	0	0	0	0	0	1	0	0	-	0	1	1	
<i>Colletes petropolitanus</i>	1	0	3	0	1	1	1	1	1	1	1	2	1	1	2	1	?	0	0	0	0	0	0	-	0	1	1	
<i>Colletes rufipes</i>	2	0	3	0	1	1	1	1	1	1	1	3	0	1	2	0	0	0	0	0	0	0	0	-	0	1	1	
<i>Colletes simulans</i>	2	0	3	0	1	1	1	1	1	1	1	2	0	1	2	0	0	0	0	0	0	0	0	-	0	1	1	
<i>Colletes succinctus</i>	3	0	4	0	1	1	1	1	1	1	2	2	2	1	2	0	0	0	0	0	1	0	1	0	0	1	1	
<i>Hemicotelles magallanes</i>	1	1	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	1	1	0	
<i>Hemicotelles ruizii</i>	1	1	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	1	1	0	
<i>Mourecotelles boliviensis</i>	1	1	1	0	0	-	0	-	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0	-	1	1	0	
<i>Mourecotelles chillan</i>	1	1	0	0	0	-	0	-	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0	-	1	0	-	
<i>Mourecotelles enodis</i>	1	1	0	0	0	-	0	-	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0	-	1	1	0	
<i>Mourecotelles mixtus</i>	1	0	0	0	0	-	0	-	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0	-	1	1	0	
<i>Mourecotelles mondelkei</i>	1	1	0	0	0	-	0	-	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0	-	1	1	0	
<i>Mourecotelles puelche</i>	1	1	0	0	0	-	0	-	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0	-	1	0	-	
<i>Mourecotelles</i> sp.	1	1	0	0	0	-	0	-	0	-	1	0	0	1	1	0	1	0	0	0	0	0	0	-	1	1	0	
<i>Mourecotelles spinolae</i>	1	1	0	0	0	-	0	-	0	-	1	0	0	1	1	0	0	0	0	0	0	0	1	2	1	1	0	
<i>Rhynchocolletes albicinctus</i>	1	1	0	0	1	0	1	1	1	1	1	0	2	1	1	0	0	1	0	0	2	0	1	4	0	1	1	
<i>Xanthocolletes adesmiae</i>	1	1	0	0	0	-	0	-	0	-	1	0	0	1	1	1	1	0	0	0	0	0	1	2	1	1	0	
<i>Xanthocolletes aisen</i>	1	1	1	0	0	-	0	-	0	-	2	1	0	1	1	1	1	0	0	0	0	1	1	4	1	1	0	
<i>Xanthocolletes andinus</i>	1	0	0	0	0	-	0	-	0	-	1	0	0	1	1	1	1	0	0	0	0	0	1	2	1	1	0	
<i>Xanthocolletes atacama</i>	1	0	0	0	0	-	0	-	0	-	1	0	0	1	1	1	1	0	0	0	0	0	0	-	1	1	0	
<i>Xanthocolletes basitarsis</i>	1	1	1	0	0	-	0	-	0	-	1	0	0	1	1	0	1	0	0	0	0	1	1	3	1	1	0	
<i>Xanthocolletes fritzi</i>	1	1	1	0	0	-	0	-	0	-	1	0	0	1	1	1	1	0	0	0	0	0	0	-	1	1	0	
<i>Xanthocolletes incahuasi</i>	1	1	1	0	0	-	0	-	0	-	1	1	0	1	1	1	1	0	0	0	0	0	1	0	1	1	0	
<i>Xanthocolletes sicheli</i>	1	0	1	0	0	-	0	-	0	-	1	0	0	1	1	1	1	0	0	0	0	0	1	2	1	1	0	
<i>Xanthocolletes subandinus</i>	1	0	0	0	0	-	0	-	0	-	1	0	0	1	1	1	1	0	0	0	0	1	1	0	1	0	-	
<i>Xanthocolletes tarsalis</i>	1	1	1	0	0	-	0	-	0	-	1	0	0	1	1	0	1	0	0	0	0	1	1	3	1	1	0	

Species	Characters																										
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	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
<i>Mydrosoma sabarensis</i>	-	0	1	1	1	1	0	0	-	1	0	0	0	1	2	0	-	-	-	-	-	0	-	2	2	-	0
<i>Euhesma sybilae</i>	-	0	0	0	0	0	0	0	-	1	0	0	2	0	-	-	-	-	-	-	0	-	2	2	-	0	
<i>Xanthesma megastigma</i>	-	0	0	1	0	0	0	0	-	0	0	0	2	1	0	1	-	-	-	-	-	1	1	2	2	-	0
<i>Hylaeus modestus</i>	-	1	0	0	1	2	0	0	-	0	0	0	2	1	0	2	-	-	-	-	-	1	1	2	2	-	1
<i>Hyleoides concinna</i>	-	0	0	0	2	2	1	0	-	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hexanthesa entrerriana</i>	-	0	1	0	1	1	0	0	-	0	0	0	2	1	1	1	-	-	-	-	-	0	-	0	2	-	0
<i>Trichocolletes dowerinensis</i>	-	0	1	1	1	1	0	0	-	0	0	0	1	1	1	1	-	-	-	-	-	0	-	0	2	-	0
<i>Scrapter heterodoxus</i>	-	0	1	1	1	2	0	0	-	0	0	0	2	1	0	0	-	-	-	-	-	0	-	2	2	-	0
<i>Scrapter spinipes</i>	-	1	1	0	2	2	0	0	-	0	0	0	2	0	-	-	-	-	-	-	-	0	-	2	2	-	0
<i>Chilicola herbsti</i>	-	1	0	0	1	2	0	0	-	0	0	0	2	1	0	1	-	-	-	-	-	1	0	0	1	-	1
<i>Xenochilicola diminuta</i>	-	1	0	0	1	2	0	0	-	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Colletes albomaculatus</i>	1	1	1	1	2	2	0	0	-	0	0	3	3	1	0	3	0	0	0	0	0	1	1	2	0	0	2
<i>Colletes americanus</i>	0	1	1	1	0	0	0	1	1	0	1	3	3	1	0	3	1	0	1	0	0	1	1	1	0	1	2
<i>Colletes atripes</i>	0	1	1	2	0	0	0	0	-	0	0	0	3	1	0	3	1	0	0	0	0	1	1	1	0	0	2
<i>Colletes bombiformis</i>	1	1	1	3	0	0	0	0	-	0	0	0	3	1	0	3	0	0	0	0	0	1	1	1	0	1	2
<i>Colletes capensis</i>	0	1	1	0	1	3	0	1	1	0	1	3	3	1	0	3	1	0	0	1	0	1	1	1	0	1	2
<i>Colletes chusmiza</i>	1	1	1	1	1	1	0	0	-	1	0	0	3	1	0	3	2	0	0	0	0	1	1	2	0	0	2
<i>Colletes clypeonitens</i>	-	1	1	0	1	1	0	1	1	0	1	4	3	1	0	3	1	0	0	0	0	1	1	2	0	0	2
<i>Colletes compactus</i>	0	1	1	0	2	3	0	1	1	0	1	4	3	1	0	3	1	0	0	0	0	1	1	2	0	0	2
<i>Colletes coriandri</i>	0	1	1	0	1	1	0	1	0	0	0	4	3	1	0	3	1	0	0	0	0	1	1	1	0	0	2
<i>Colletes cyanescens</i>	-	1	1	0	0	0	0	0	-	1	0	4	3	1	0	3	1	0	0	0	0	1	1	2	0	1	2
<i>Colletes eous</i>	0	1	1	1	3	2	1	1	1	0	1	3	3	1	0	3	2	0	0	0	0	1	1	2	0	0	2
<i>Colletes eulophi</i>	0	1	1	1	1	2	0	1	1	0	1	3	3	1	0	3	0	0	1	0	0	1	1	2	0	0	2
<i>Colletes gilvus</i>	0	1	1	0	1	1	0	1	1	0	1	3	3	1	0	3	0	0	0	1	0	1	1	2	0	0	2
<i>Colletes graeffei</i>	0	1	1	1	1	3	0	1	1	0	1	4	3	1	0	3	1	0	0	1	0	1	1	1	0	1	2
<i>Colletes hirtibasis</i>	0	1	1	0	1	2	0	1	1	0	0	3	3	1	0	3	0	0	0	0	0	1	1	2	0	0	1
<i>Colletes hyalinus</i>	0	1	1	0	0	1	0	1	0	0	1	3	3	1	0	3	1	0	1	0	0	1	1	2	0	0	2
<i>Colletes impunctatus</i>	0	1	1	1	1	2	0	1	1	0	0	3	3	1	0	3	0	2	0	0	0	1	1	2	0	1	2
<i>Colletes inaequalis</i>	0	1	1	1	1	3	0	1	1	0	1	4	3	1	0	3	1	0	1	0	0	1	1	1	0	0	2
<i>Colletes inexpectatus</i>	0	1	1	1	1	2	0	1	1	0	1	4	3	1	0	3	1	1	1	0	0	1	1	1	0	0	2
<i>Colletes kozlovi</i>	0	1	1	1	1	2	0	1	1	0	0	3	3	1	0	3	0	0	0	0	0	1	1	1	0	0	2

Species	Characters																										
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	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3		
	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
<i>Colletes lacunatus</i>	0	1	1	1	3	3	1	1	1	0	1	3	3	1	0	3	0	0	0	0	0	1	1	1	0	0	2
<i>Colletes nasutus</i>	0	1	1	0	1	2	0	1	1	0	0	3	3	1	0	3	0	0	1	0	0	1	1	2	0	0	1
<i>Colletes nigrifrons</i>	1	1	1	3	0	0	0	1	0	0	0	0	3	1	0	3	0	0	0	0	0	1	1	2	0	0	2
<i>Colletes nigrutilus</i>	0	1	1	0	0	1	0	1	1	0	1	3	3	1	0	3	1	0	1	0	0	1	1	2	0	0	2
<i>Colletes perileucus</i>	0	1	1	0	0	0	0	1	1	0	0	3	3	1	0	3	1	0	0	0	0	1	1	1	0	0	2
<i>Colletes petropolitanus</i>	0	1	1	1	0	2	0	1	1	0	0	3	3	1	0	3	0	0	0	0	0	1	1	1	0	0	2
<i>Colletes rufipes</i>	0	1	1	1	1	2	0	1	0	0	1	3	3	1	0	3	1	0	0	0	0	1	1	2	0	0	2
<i>Colletes simulans</i>	0	1	1	1	1	3	0	1	1	0	1	3	3	1	0	3	0	0	0	1	0	1	1	2	0	0	2
<i>Colletes succinctus</i>	0	1	1	?	3	3	1	?	?	0	1	3	3	1	0	3	0	0	0	0	0	1	1	1	0	0	2
<i>Hemicotelles magallanes</i>	-	0	1	1	0	2	0	1	1	0	0	1	3	1	0	3	0	0	0	0	0	1	1	1	0	0	2
<i>Hemicotelles ruizii</i>	-	0	1	1	0	2	0	1	0	0	0	1	3	1	0	3	0	0	0	0	0	1	1	1	0	0	2
<i>Mourecotelles boliviensis</i>	-	0	1	1	0	0	0	1	0	0	0	2	3	1	0	3	1	0	1	0	0	1	0	2	0	0	2
<i>Mourecotelles chillan</i>	-	0	1	1	0	1	0	0	-	0	0	0	3	1	0	3	1	0	1	0	0	1	0	2	0	0	2
<i>Mourecotelles enodis</i>	-	0	1	1	0	1	0	0	-	0	0	0	3	1	0	3	1	0	1	0	0	1	0	2	0	0	2
<i>Mourecotelles mixtus</i>	-	0	1	1	0	1	0	0	-	0	0	0	3	1	0	3	1	0	1	0	0	1	0	2	0	0	2
<i>Mourecotelles mondelkei</i>	-	0	1	1	0	2	0	0	-	0	0	0	3	1	0	3	1	0	1	0	0	1	0	2	0	0	2
<i>Mourecotelles puelche</i>	-	0	1	1	0	1	0	0	-	0	0	0	3	1	0	3	1	0	1	0	0	1	0	2	0	0	2
<i>Mourecotelles sp.</i>	-	0	1	1	0	2	0	1	1	0	0	1	3	1	0	3	1	0	1	0	0	1	0	2	0	0	2
<i>Mourecotelles spinolae</i>	-	0	1	2	0	2	0	1	1	0	0	3	3	1	0	3	1	0	1	0	0	1	0	2	2	0	2
<i>Rhynchocolletes albicinctus</i>	1	1	1	1	1	2	0	0	-	1	0	1	3	1	0	3	1	0	1	0	0	0	-	2	0	0	2
<i>Xanthocolletes adesmiae</i>	-	0	1	1	0	0	0	1	1	0	0	4	3	1	0	3	0	0	0	0	0	1	0	2	0	1	2
<i>Xanthocolletes aisen</i>	-	0	1	1	0	1	0	0	-	0	0	5	3	1	0	3	0	0	1	0	0	1	0	2	0	1	2
<i>Xanthocolletes andinus</i>	-	0	1	1	0	0	0	1	1	0	0	4	3	1	0	3	0	0	1	0	0	1	0	2	0	1	2
<i>Xanthocolletes atacama</i>	-	0	1	1	0	0	0	1	1	0	0	4	3	1	0	3	0	0	1	0	1	1	0	2	0	1	2
<i>Xanthocolletes basitarsis</i>	-	1	1	1	0	0	0	0	-	0	0	5	3	1	0	3	0	0	1	0	0	1	0	2	0	0	2
<i>Xanthocolletes fritzi</i>	-	0	1	1	0	0	0	1	1	0	0	4	3	1	0	3	0	0	0	0	0	1	0	2	0	1	2
<i>Xanthocolletes incahuasi</i>	-	0	1	1	0	0	0	1	1	0	0	4	3	1	0	3	1	0	1	0	0	1	0	2	0	1	2
<i>Xanthocolletes sicheli</i>	-	0	1	1	0	0	0	1	1	0	0	4	3	1	0	3	0	0	1	0	1	1	0	2	0	1	0
<i>Xanthocolletes subandinus</i>	-	0	1	1	0	1	0	1	1	0	0	5	3	1	0	3	0	0	1	0	0	1	0	2	0	1	2
<i>Xanthocolletes tarsalis</i>	-	1	1	1	0	0	0	0	-	0	0	4	3	1	0	3	0	0	1	0	0	1	0	2	0	0	2



Species	Characters													
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	6	7	8	9	0	1	2	3	4	5	6	7	8	9
<i>Mydrosoma sabarensis</i>	0	0	0	0	0	0	0	1	2	0	1	0	0	0
<i>Euhesma sybilae</i>	0	1	0	0	0	0	0	0	-	-	-	0	0	0
<i>Xanthesma megastigma</i>	0	1	0	0	0	0	0	0	-	-	-	0	0	0
<i>Hylaeus modestus</i>	0	0	0	0	0	0	0	0	-	-	-	0	0	0
<i>Hyleoides concinna</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hexanthesa entrerriana</i>	0	0	0	0	0	0	0	0	-	-	-	0	0	0
<i>Trichocolletes dowerinensis</i>	0	0	0	0	0	0	0	0	-	-	-	0	1	0
<i>Scrapter heterodoxus</i>	0	0	0	1	0	0	0	1	2	0	1	0	0	0
<i>Scrapter spinipes</i>	0	0	0	1	0	0	0	1	2	2	1	0	0	0
<i>Chilicola herbsti</i>	0	0	0	0	0	0	0	0	-	-	-	0	0	0
<i>Xenochilicola diminuta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Colletes albomaculatus</i>	0	1	0	0	1	0	0	1	2	4	1	0	0	0
<i>Colletes americanus</i>	0	1	0	0	1	0	0	1	1	1	1	0	0	0
<i>Colletes atripes</i>	0	1	0	0	1	0	0	1	1	2	1	0	1	0
<i>Colletes bombiformis</i>	0	2	0	0	1	0	0	1	2	4	0	0	0	0
<i>Colletes capensis</i>	0	1	0	0	1	0	0	1	2	4	0	0	0	0
<i>Colletes chusmiza</i>	0	1	0	0	1	0	0	1	1	1	0	1	1	1
<i>Colletes clypeonitens</i>	0	1	0	0	1	0	0	1	0	4	0	0	0	0
<i>Colletes compactus</i>	0	1	0	0	1	0	0	1	1	2	0	0	0	0
<i>Colletes coriandri</i>	0	1	0	0	1	0	0	1	1	3	0	1	0	0
<i>Colletes cyanescens</i>	0	1	0	0	1	0	0	1	1	4	0	0	0	0
<i>Colletes eous</i>	0	1	0	0	0	0	0	1	3	4	1	0	0	1
<i>Colletes eulophi</i>	0	1	0	0	1	0	0	1	0	1	0	0	0	0
<i>Colletes gilvus</i>	0	1	0	0	1	0	0	1	1	2	1	1	1	0
<i>Colletes graeffei</i>	0	1	0	0	1	0	0	1	2	4	0	1	0	0
<i>Colletes hirtibasis</i>	0	1	0	0	1	0	0	1	1	2	1	0	0	0
<i>Colletes hyalinus</i>	0	1	0	0	1	0	0	1	1	4	0	0	0	1
<i>Colletes impunctatus</i>	0	2	0	0	1	0	0	1	1	1	1	0	0	0
<i>Colletes inaequalis</i>	0	2	0	0	1	0	0	1	1	4	0	0	0	0
<i>Colletes inexpectatus</i>	0	1	0	0	0	0	0	1	2	4	0	0	0	0
<i>Colletes kozlovi</i>	0	2	0	0	1	0	0	1	2	4	1	0	0	0

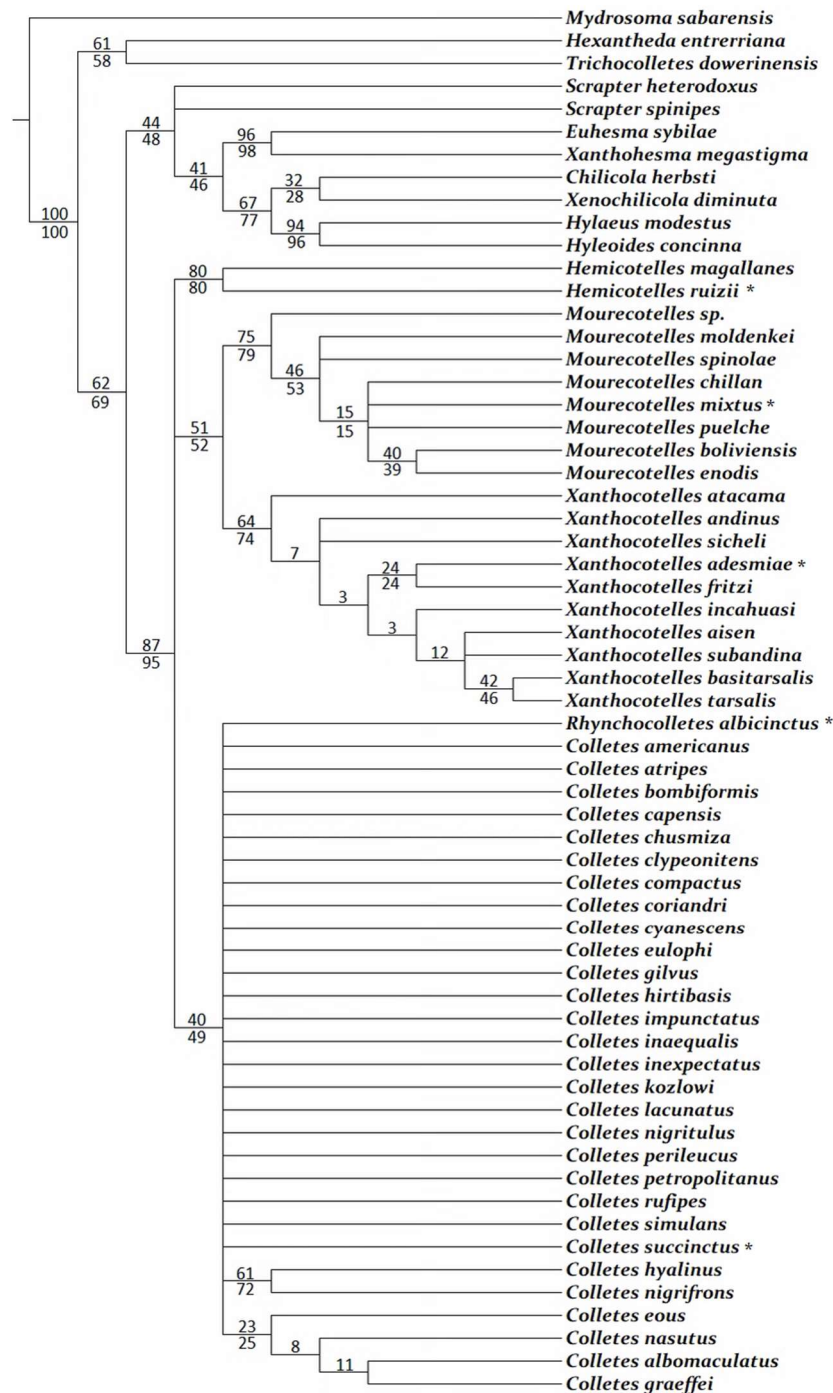
Species	Characters													
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	6	7	8	9	0	1	2	3	4	5	6	7	8	9
<i>Colletes lacunatus</i>	0	1	0	0	1	0	0	1	3	4	0	0	0	1
<i>Colletes nasutus</i>	0	1	0	0	1	0	0	1	1	2	1	0	0	0
<i>Colletes nigrifrons</i>	0	1	0	0	1	0	0	1	1	2	0	1	0	0
<i>Colletes nigrutilus</i>	0	2	0	0	1	0	0	1	0	2	0	0	0	0
<i>Colletes perileucus</i>	0	1	0	0	1	0	0	1	1	2	0	0	0	0
<i>Colletes petropolitanus</i>	0	1	0	0	1	0	0	1	1	2	1	1	1	0
<i>Colletes rufipes</i>	0	1	0	0	1	0	0	1	3	4	0	1	0	0
<i>Colletes simulans</i>	0	1	0	0	1	0	0	1	1	4	1	0	0	0
<i>Colletes succinctus</i>	0	2	0	0	1	0	0	1	3	4	0	1	0	0
<i>Hemicotelles magallanes</i>	0	1	0	0	1	0	0	1	1	1	1	0	1	0
<i>Hemicotelles ruizii</i>	0	1	0	0	1	0	0	1	1	1	1	0	1	0
<i>Mourecotelles boliviensis</i>	1	0	0	0	0	1	1	1	2	0	2	0	0	0
<i>Mourecotelles chillan</i>	1	0	0	0	0	1	1	1	2	0	2	0	0	0
<i>Mourecotelles enodis</i>	1	0	0	0	0	1	1	1	2	0	2	0	0	0
<i>Mourecotelles mixtus</i>	1	0	0	0	0	1	1	1	2	0	2	0	0	0
<i>Mourecotelles mondelkei</i>	1	0	0	0	0	1	1	1	2	0	2	0	0	0
<i>Mourecotelles puelche</i>	1	0	0	0	0	1	1	1	2	0	2	0	0	0
<i>Mourecotelles sp.</i>	1	0	0	0	0	1	1	1	2	0	2	0	0	0
<i>Mourecotelles spinolae</i>	0	0	0	0	0	1	1	1	0	0	2	0	0	0
<i>Rhynchocolletes albicinctus</i>	0	0	0	1	0	0	0	1	1	1	1	0	0	0
<i>Xanthocolletes adesmiae</i>	0	0	1	0	0	1	0	1	1	2	1	0	0	0
<i>Xanthocolletes aisen</i>	0	0	1	0	0	1	0	1	1	2	1	0	0	0
<i>Xanthocolletes andinus</i>	0	0	1	0	0	1	0	1	1	2	0	0	0	0
<i>Xanthocolletes atacama</i>	0	0	1	0	0	1	0	1	1	0	1	0	0	0
<i>Xanthocolletes basitarsis</i>	0	0	1	0	0	1	0	1	1	2	1	0	0	0
<i>Xanthocolletes fritzi</i>	0	0	1	0	0	1	0	1	1	2	1	0	0	0
<i>Xanthocolletes incahuasi</i>	0	0	1	0	0	1	0	1	1	2	1	0	0	0
<i>Xanthocolletes sicheli</i>	0	0	1	0	0	1	0	1	1	2	0	0	0	0
<i>Xanthocolletes subandinus</i>	0	0	1	0	0	1	0	1	1	2	1	0	0	0
<i>Xanthocolletes tarsalis</i>	0	0	1	0	0	1	0	1	1	2	1	0	0	0

**Table S4.** Continuous character matrix for the species included in the phylogenetic analyses. -: inapplicable, ?: missing data.

Species	Characters											
	150	151	152	153	154	155	156	157	158	159	160	161
<i>Mydrosoma sabarensis</i>	0.410	?	-	0.777	0.760	1.035	0.183	0.520	0.810	0.188	1.028	1.247
<i>Euhesma sybilae</i>	0.295	0.290	-	-	0.310	0.770	0.073	0.280	0.500	0.916	1.000	0.810
<i>Xanthesma megastigma</i>	0.350	0.050	-	-	0.260	0.750	0.040	0.280	0.535	1.025	0.800	1.047
<i>Hylaeus modestus</i>	0.760	0.140	-	0.557	0.330	0.667	0.100	0.345	0.520	0.714	0.742	0.643
<i>Hyleoides concinna</i>	0.875	0.165	-	0.623	0.740	1.180	0.153	0.550	?	0.544	0.900	0.571
<i>Hexanthesa entrerriana</i>	0.305	-	-	1.057	0.730	0.795	0.013	0.725	0.400	0.93	0.624	0.801
<i>Trichocolletes dowerinensis</i>	0.390	-	-	-	0.990	0.475	0.197	1.250	0.750	0.475	0.774	0.350
<i>Scrapter heterodoxus</i>	0.390	0.500	-	-	0.920	1.025	0.060	0.910	?	0.725	0.800	0.479
<i>Scrapter spinipes</i>	0.215	0.205	-	-	0.350	0.72	0.017	0.525	0.385	1.125	0.856	0.600
<i>Chilicola herbsti</i>	0.625	-	-	0.500	0.240	0.655	0.067	0.345	0.500	0.900	1.074	0.714
<i>Xenochilicola diminuta</i>	0.865	-	-	0.583	0.150	0.400	0.790	0.400	0.450	1.000	1.05	0.429
<i>Colletes albomaculatus</i>	0.577	0.375	0.305	0.943	0.800	0.865	0.140	0.540	0.675	0.515	0.674	0.571
<i>Colletes americanus</i>	0.596	0.640	0.515	0.813	0.640	0.590	0.103	0.350	0.710	0.574	0.550	0.754
<i>Colletes atripes</i>	0.729	0.795	0.360	0.667	0.730	0.600	0.733	0.550	0.725	0.458	0.578	0.510
<i>Colletes bombiformis</i>	0.557	0.550	0.585	0.620	0.730	0.805	0.140	0.375	0.875	0.509	0.622	0.463
<i>Colletes capensis</i>	0.740	0.790	0.700	0.787	0.700	0.820	0.350	0.500	0.705	0.638	0.656	0.646
<i>Colletes chusmiza</i>	0.660	0.230	0.425	0.917	0.780	0.810	0.687	0.725	0.890	0.563	0.686	0.299
<i>Colletes clypeonitens</i>	0.745	0.690	0.605	0.570	0.620	0.725	0.597	0.445	0.910	0.631	0.724	0.699
<i>Colletes compactus</i>	0.632	0.465	0.835	0.667	0.760	0.885	0.317	0.460	0.770	0.519	0.572	0.611
<i>Colletes coriandri</i>	0.648	0.390	0.575	0.587	0.770	0.725	0.373	0.525	0.685	0.614	0.696	0.680
<i>Colletes cyanescens</i>	0.724	0.320	0.275	0.587	0.790	0.805	0.667	0.675	1.000	0.576	0.820	0.583
<i>Colletes eous</i>	0.607	0.365	0.415	0.723	0.680	0.700	0.270	0.385	0.790	0.569	0.768	0.566
<i>Colletes eulophi</i>	0.633	0.300	0.600	0.833	0.600	0.640	0.230	0.415	0.695	0.524	0.620	0.614
<i>Colletes gilvus</i>	0.729	0.400	0.395	0.557	0.750	0.665	0.667	0.665	0.800	0.428	0.662	0.544
<i>Colletes graeffei</i>	0.604	0.605	0.480	1.083	0.760	0.950	0.093	0.430	0.600	0.500	0.688	0.364
<i>Colletes hirtibasis</i>	0.604	0.565	0.665	1.523	0.700	0.600	0.177	0.375	0.790	0.588	0.628	0.700
<i>Colletes hyalinus</i>	0.596	0.885	0.675	0.723	0.570	0.875	0.093	0.440	0.615	0.541	0.734	0.417
<i>Colletes impunctatus</i>	0.654	0.460	0.540	0.727	0.630	0.690	0.290	0.445	0.740	0.585	0.722	0.500
<i>Colletes inaequalis</i>	0.544	0.435	0.545	0.587	0.810	0.770	0.190	0.440	0.710	0.670	0.696	0.679
<i>Colletes inexpectatus</i>	0.553	0.500	0.500	0.933	0.610	0.770	0.147	0.440	0.625	0.575	0.820	0.423
<i>Colletes kozlovi</i>	0.631	0.640	0.570	0.750	0.550	0.605	0.127	0.410	0.780	0.695	0.760	0.660
<i>Colletes lacunatus</i>	0.589	1.000	0.530	0.857	0.890	0.905	0.320	0.480	0.795	0.568	0.702	0.669

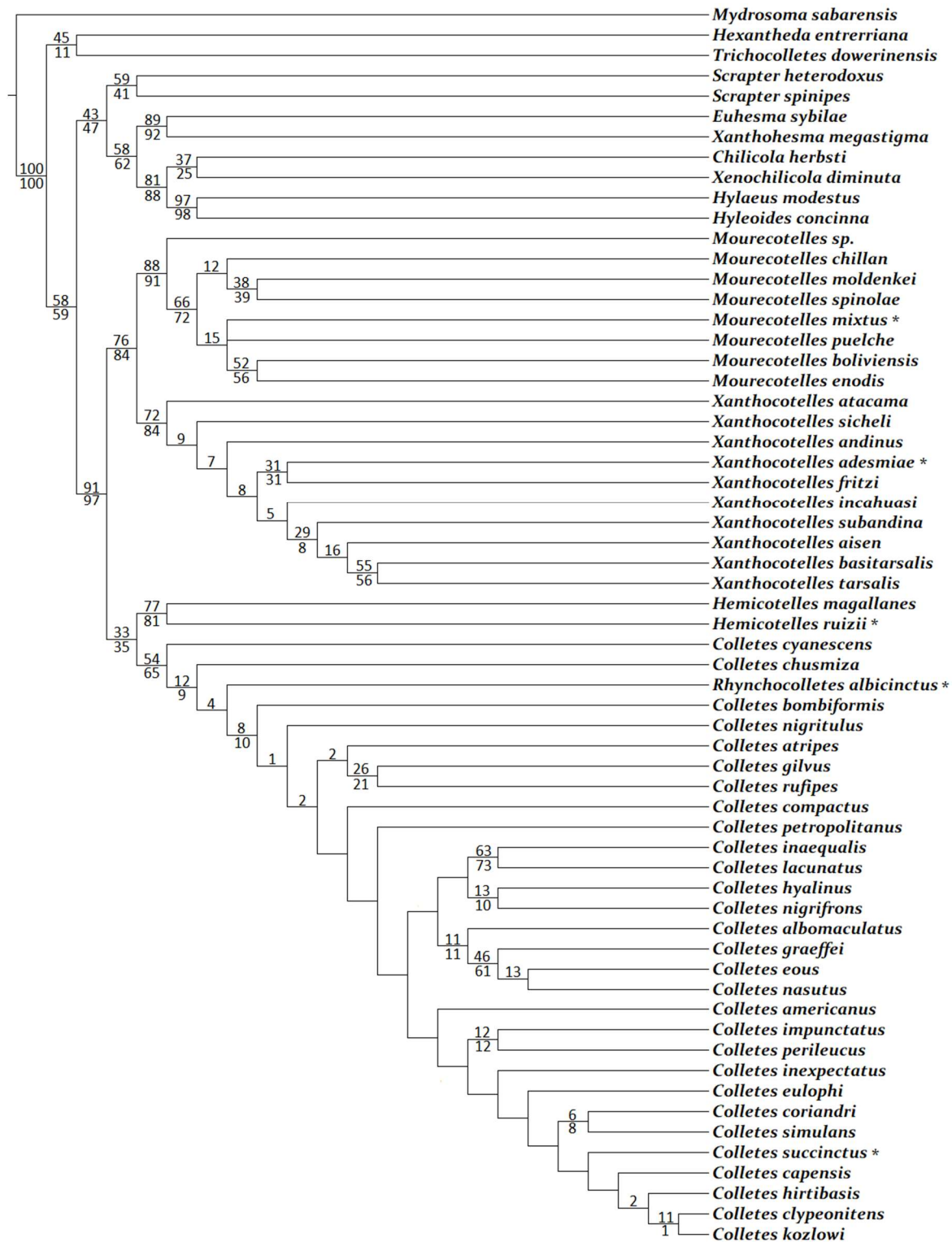
Species	Characters											
	150	151	152	153	154	155	156	157	158	159	160	161
<i>Colletes nasutus</i>	0.816	0.720	0.470	1.267	0.750	0.760	0.667	0.475	0.630	0.429	0.606	0.676
<i>Colletes nigrifrons</i>	0.614	0.365	0.640	0.727	0.520	0.825	0.137	0.470	0.545	0.486	0.700	0.453
<i>Colletes nigrifulus</i>	0.555	0.640	0.285	1.167	0.710	0.885	0.333	0.475	0.730	0.575	0.970	0.607
<i>Colletes perileucus</i>	0.656	0.440	0.515	0.470	0.760	0.870	0.167	0.430	0.745	0.469	0.556	0.547
<i>Colletes petropolitanus</i>	0.585	0.925	0.885	0.547	0.570	0.770	0.213	0.470	0.695	0.545	0.670	0.480
<i>Colletes rufipes</i>	0.698	0.500	0.550	1.110	0.670	0.595	0.807	0.525	0.640	0.500	0.646	0.653
<i>Colletes simulans</i>	0.577	0.550	0.500	0.843	0.710	0.815	0.107	0.430	0.715	0.523	0.612	0.640
<i>Colletes succinctus</i>	0.593	0.605	0.480	1.083	0.680	0.775	0.217	0.475	0.655	0.568	0.752	0.714
<i>Hemicotelles magallanes</i>	0.632	0.675	0.590	-	0.840	0.695	0.683	0.565	0.835	0.428	0.800	0.520
<i>Hemicotelles ruizii</i>	0.653	0.615	0.595	-	0.930	0.705	0.693	0.615	0.855	0.438	0.738	0.433
<i>Mourecotelles boliviensis</i>	0.758	0.355	-	0.667	0.760	0.885	0.737	0.750	0.675	0.476	0.500	0.416
<i>Mourecotelles chillan</i>	0.710	0.285	-	0.717	0.780	0.960	0.490	0.760	0.665	0.455	0.626	0.446
<i>Mourecotelles enodis</i>	0.700	0.320	-	0.717	0.790	1.085	0.767	0.840	0.685	0.389	0.574	0.433
<i>Mourecotelles mixtus</i>	0.789	0.320	-	0.777	0.780	0.925	0.870	0.680	0.715	0.380	0.550	0.420
<i>Mourecotelles mondelkei</i>	0.896	0.280	-	0.727	0.760	0.865	0.940	0.870	0.765	0.443	0.580	0.451
<i>Mourecotelles puelche</i>	0.755	0.305	-	0.667	0.820	1.040	0.697	0.750	0.660	0.438	0.588	0.361
<i>Mourecotelles sp.</i>	0.861	0.305	-	0.953	0.770	0.885	0.740	0.800	0.790	0.420	0.586	0.451
<i>Mourecotelles spinolae</i>	0.808	0.300	-	0.760	0.860	0.915	0.493	0.900	0.560	0.343	0.618	0.547
<i>Rhynchocolletes albicinctus</i>	?	?	?	?	0.860	0.685	0.833	0.700	0.820	0.531	0.646	0.279
<i>Xanthocotelles adesmiae</i>	0.750	0.385	-	-	0.730	1.020	0.477	0.620	0.745	0.398	0.654	0.397
<i>Xanthocotelles aisen</i>	0.731	0.375	-	-	0.740	1.020	0.667	0.610	0.875	0.488	0.758	0.306
<i>Xanthocotelles andinus</i>	0.755	0.270	-	-	0.670	0.950	0.743	0.650	0.770	0.339	0.520	0.467
<i>Xanthocotelles atacama</i>	0.709	0.290	-	-	0.690	0.890	0.537	0.600	0.820	0.431	0.572	0.480
<i>Xanthocotelles basitarsis</i>	?	?	-	-	0.640	0.915	0.743	0.685	0.805	0.413	0.592	0.349
<i>Xanthocotelles fritzi</i>	0.761	0.375	-	-	0.730	0.920	0.473	0.650	0.680	0.398	0.510	0.429
<i>Xanthocotelles incahuasi</i>	0.709	0.270	-	-	0.690	0.875	0.627	0.700	0.685	0.409	0.592	0.383
<i>Xanthocotelles sicheli</i>	0.783	0.335	-	-	0.660	0.825	0.770	0.775	0.750	0.330	0.646	0.449
<i>Xanthocotelles subandinus</i>	?	?	-	-	0.680	0.865	0.790	0.630	0.750	0.440	0.734	0.326
<i>Xanthocotelles tarsalis</i>	?	?	-	-	0.650	1.000	0.650	0.775	0.720	0.488	0.672	0.341

## Appendix II: Supplementary figures



**Figure S1.** Strict consensus of the 92 most parsimonious trees from the equal weights analysis carried out with only the discrete characters. Numbers above internodes are absolute values from bootstrapping and below are GC ratios (negative values not shown) from symmetric resampling. Asterisks indicate type species of the genus.





**Figure S2.** Fittest tree from the implied weighting analysis carried out with only the discrete characters. Numbers above internodes are absolute values from bootstrapping and below are GC ratios (negative values not shown) from symmetric resampling. Asterisks indicate type species of the genus.

### Chapter 3: Taxonomic revision of the species of *Colletes* Latreille, 1802 (Hymenoptera: Colletidae: Colletinae) found in Chile<sup>1</sup>

Rafael R. Ferrari

#### Abstract

A taxonomic revision of *Colletes* Latreille species with known geographic distribution in Chile is presented. In addition to the traditional morphological approach to taxonomy, DNA barcoding was employed to facilitate sexual association and cryptic species recognition. I provide diagnoses, synonymies, geographic and floral records, and a fully-illustrated key for 31 recognized species, 23 of them previously described: *C. alocochila* Moure, *C. atacamensis* Janvier, *C. atripes* Smith, *C. bicolor* Smith, *C. chusmiza* Rojas & Toro, *C. cognatus* Spinola, *C. cyanescens* (Haliday), *C. cyaniventris* Spinola **n. stat.**, *C. flaminii* Moure, *C. fulvipes* Spinola, *C. gilvus* Vachal, *C. guanta* Rojas & Toro, *C. longiceps* Friese, *C. lucens* Vachal, *C. mastochila* Moure, *C. murinus* Friese, *C. musculus* Friese, *C. nigrutilus* Friese, *C. patagonicus* Schrottky, *C. quelu* Rojas & Toro, *C. rutilans* Vachal, *C. sulcatus* Vachal, and *C. vicugnensis* Rojas & Toro. In addition, eight new species are described: *C. arthuri* **n. sp.**, *C. coquimbensis* **n. sp.**, *C. flavipilosus* **n. sp.**, *C. kuhlmanni* **n. sp.**, *C. nigropilosus* **n. sp.**, *C. simulatus* **n. sp.**, *C. toroi* **n. sp.**, and *C. ventricarinatus* **n. sp.** Lectotypes for the following species are designated: *Andrena cyanescens*, *Colletes bicolor*, *C. campoi* Herbst, *C. chubutensis* Cockerell, *C. gilvus*, *C. lucens*, *C. patagonicus*, *C. rufosignatus* Cockerell, and *C. viridans* Vachal. *Colletes seminitidus* Spinola and *C. viridans* are both proposed as junior synonyms of *C. cyanescens*, and *C. araucariae* Friese is considered a junior synonym of *C. sulcatus*. *Colletes cyaniventris* **n. stat.** is resurrected from synonymy.

<sup>1</sup>This manuscript and all of its images have been published in, and are copyrighted by, *Zootaxa* and are reprinted here with the journal's permission:

Ferrari, R.R. (2017) Taxonomic revision of the species of *Colletes* Latreille, 1802 (Hymenoptera: Colletidae: Colletinae) found in Chile. *Zootaxa*, 4364, 1–137.

Available at: <http://www.mapress.com/j/zt>

## Introduction

*Colletes* Latreille, 1802 is the only genus of Colletinae (Hymenoptera: Apoidea: Colletidae) with a worldwide distribution, absent in Oceania only (Michener 2007), although its occurrence in southeast Asia has been reported only recently (Kuhlmann 2014). As with many bee groups, *Colletes* is more diverse in xeric environments (e.g. Michener 1979, Patiny & Michez 2007), such as the southwestern United States, central Asia and the Chilean Atacaman province (sensu Morrone 2014). Species are solitary and usually nest (in many cases gregariously) in bare sandy soils (Torchio *et al.* 1988), although at least one Brazilian species – *C. rufipes* Smith, 1879 – has also been found nesting in bamboo trap nests (Gazola & Garófalo 2009).

Currently, 495 valid *Colletes* species are accepted (Ascher & Pickering 2017), from an estimated 700 (Kuhlmann *et al.* 2009). In South America, where the genus is thought to have originated (Michener 1979, 2007; Kuhlmann *et al.* 2009; Almeida *et al.* 2011), *Colletes* is represented by 70 described species (Moure *et al.* 2007). Since the seminal paper by Noskiewicz (1936), who revised the Palaearctic species, numerous taxonomic revisions of the genus have been published [e.g. America north of Mexico (Stephen 1954), western Palaearctic (Warncke 1978), Japan (Ikudome 1989), Russia (Kuhlmann & Proshchalykin 2011), Ukraine (Proshchalykin & Kuhlmann 2012), central Asia (Kuhlmann & Proshchalykin 2013, 2014), Ethiopia (Kuhlmann & Pauly 2013), China (Niu *et al.* 2014), and the Caucasus (Kuhlmann & Proshchalykin 2016)]. In contrast, the South American fauna of *Colletes* has never been the subject of a comprehensive taxonomic revision (Michener 2007).

Chile is a narrow, long country bordered to the west and south by the Pacific Ocean, to the east by the Andes and to the north by the Atacaman desert (Moreira-Muñoz 2011). These nearly impassible barriers coupled with its complex climate and physical geography result in very high levels of endemism (e.g. Cracraft 1985; Smith-Ramírez 2004), making the Chilean biota particularly interesting on taxonomic and biogeographic grounds. In fact, 300 of the 424 (~70%) bee species known to occur in Chile are endemic to the country (Montalva & Ruz 2010).

In an early checklist of the bee species found in Chile (Ruiz 1944), 14 *Colletes* species were reported from the country (although two of them have been later moved to other genera). Toro (1986) raised this number to 21, including the species that had been described by Janvier

(1955) and Moure (1956), and some that were previously known to occur only in neighbouring countries. The most comprehensive study dealing with the Chilean fauna of *Colletes* up to now is that of Toro (1999), who provided taxonomic notes, geographic and floral records, and identification keys for 23 species, including the ones described previously by Rojas & Toro (1993). Nevertheless, examination of 1,583 specimens of the genus collected in Chile made clear that the identity of some species cannot be unambiguously identified with the key provided by Toro (1999), and that some cryptic species remain undescribed.

The present study is an attempt to solve the taxonomic impediments associated with the *Colletes* found in Chile. Here, I provide diagnoses, descriptions (or redescrptions) and illustrated identification keys for 31 recognized species, including eight described as new. This is the first revision of a series that aims to revise the entire South American *Colletes* fauna.

## **Materials and Methods**

### *Specimens studied*

Specimens of *Colletes* collected in Chile and neighbouring countries and deposited at the following collections were studied: Argentina – Museo Argentino de Ciencias Naturales, Buenos Aires (MACN). Brazil – Coleção Camargo, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Ribeirão Preto (RPSP); Departamento de Zoologia, Universidade Federal do Paraná, Curitiba (DZUP). Canada – Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa (CNC); Packer Collection, York University, Toronto (PCYU). Chile – Pontificia Universidad Católica de Valparaíso, Valparaíso (PUCV). England – The Natural History Museum, London (NHM). France – Muséum National d'Histoire Naturelle, Paris (MNHP). Germany – Museum für Naturkunde, Berlin (ZMB). United States – American Museum of Natural History, New York (AMNH); Division of Entomology, University of Kansas, Lawrence (KUNHM); Essig Museum of Entomology, University of California, Berkeley (EMEC); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); National Museum of Natural History, Smithsonian Institution, Washington DC (USNM); United States National Pollinating Insects Collection, Utah State University, Logan (BBSL). Other collections mentioned in this study are:

Argentina – Museo de La Plata, La Plata (MLP). Italy – Museo Regionale di Scienze Naturali, Torino (MRSN).

Data from the labels of the primary type specimens are transcribed exactly as they are given, as follows: information on a single label is given between quotation marks; the end of each line in a label is indicated by a semicolon. Data from the labels of other specimens (including secondary type specimens) are reproduced as follows: **COUNTRY – country’s first-level administrative division:** municipality or specific locality, (geographic coordinates), altitude, collection date as “dd/mm in Roman numbers/yyyy”, [collector], number of specimens of each sex, {repository institution}.

### *Sorting and taxonomic decisions*

Specimens were studied under an Olympus SZ61 stereomicroscope (maximum magnification of 75x) with a Neewer Ring48 LED ring light and sorted into operational taxonomic units (OTU's; *i.e.* putative species). I extracted the terminalia of males previously relaxed overnight, which were then cleared in 10% KOH solution and stored in glycerin in genitalia vials. The recognized OTU's were tentatively identified with the available keys (*e.g.* Rojas & Toro 1993; Toro 1999), and through comparison with the original descriptions of South American species of *Colletes*. Final decisions on species identities were ultimately based upon examination of the primary type specimens, the majority of which were examined; the exceptions are those deposited at the MRSN – *C. dimidiata* Spinola, 1851, *C. cognatus* Spinola, 1851, *C. cyaniventris* Spinola, 1851, and *C. seminitidus* Spinola, 1851 – which has been closed and its holdings therefore inaccessible over recent years (M. Garzena, *pers. comm.*), and the syntypes of *C. atacamensis* Janvier, 1955 that have been suggested to be deposited at the MNHP (Moure & Urban 2002: 4) but could not be located (A. Touret-Alby, *pers. comm.*). In the cases where examination of the primary type specimen was not possible, the rationale behind determination of species' identity is provided in the relevant “comments” section.

Herein, the International Commission on Zoological Nomenclature is referred to as “ICZN”, and the 4<sup>th</sup> edition of the International Code of Zoological Nomenclature is abbreviated as “the Code” (ICZN 1999).



## DNA barcoding

To facilitate sexual association and species delimitation, the 658-pb region of cytochrome *c* oxidase I (COI) – the primary DNA barcoding for animals (Ratnasingham & Hebert 2007) – was sequenced. This integrative approach (*i.e.* morphological scrutiny in combination with DNA barcoding) has recently become popular among bee taxonomists (*e.g.* Gibbs 2009a, b, 2010, 2011; Pauly *et al.* 2014; Hogendoorn *et al.* 2015; Rocha-Filho & Packer 2015). For DNA extraction, the right mid or hind leg of the bees was removed with sterilized forceps and stored in absolute ethanol. Then, the samples were shipped to the Canadian Centre for DNA Barcoding at the University of Guelph (Guelph, ON), where all DNA-related procedures (*i.e.* extraction, amplifying, and sequencing) were done. Finally, the resulting sequences were uploaded to the Barcode of Life Data System (BOLD) database (Ratnasingham & Herbert 2007). The collection data of the barcoded specimens are given in Table S1.

The obtained DNA barcodes were clustered in OTU's through two distinct analyses. First, all good-quality sequences (*i.e.* at least 500-pb long with less than five ambiguous bases) were automatically assigned a Barcode Index Number (BIN) (Ratnasingham & Herbert 2013). Then, on the BOLD workbench, the sequences were aligned with MUSCLE (Edgar 2004) and a neighbour joining tree (Saitou & Nei 1987) generated using the Kimura 2 Parameter (Kimura 1980) nucleotide substitution model.

An extensive study that calculated the COI divergence of 13,320 congeneric pairs of species from all major animal phyla showed that >98% of all pairs had >2% sequence divergence, and that intraspecific divergence is rarely >1% (Hebert *et al.* 2003). However, this has also been demonstrated not to be the case for numerous organisms (*e.g.* Trewick 2007), including bees (*e.g.* Kuhlmann *et al.* 2007; Gibbs 2009b). Therefore, morphology was given precedence over DNA barcodes, and the following premises were adopted throughout: (i) if two or more morphologically recognizable OTU's were grouped in the same BIN by the barcode tree, they were nonetheless treated as distinct species; and (ii) when intraspecific DNA variation was notably high but additional morphological scrutiny did not provide corresponding support, a single species was considered (see Gibbs 2010 for a similar approach).

### *Species descriptions and redescrptions*

Terminology for bee morphology is that of Michener (2007), with the following exceptions: (i) the basal and posterior surfaces of the metapostnotum are referred to as horizontal and vertical surfaces of the metapostnotum, respectively; and (ii) gena, frons and vertex are called genal, frontal and vertexal areas, respectively (following Prentice 1998, see also Packer 2008). Leg surfaces were named in accordance with Aguiar & Gibson (2010). Terminology for surface sculpture is that of Harris (1979). Metasomal terga and sterna, and antennal flagellomeres are referred to with the letters T, S, and F, respectively, followed by appropriate numbers. Upper and lower interocular distances were abbreviated as UID and LID, respectively.

Puncture spacing is given in terms of the relative sizes of the interspaces ( $i$ ) and puncture diameters ( $d$ ), as follows: sparsely punctate ( $i > 2d$ ); moderately sparsely punctate ( $i = 1.5-2d$ ); moderately densely punctate ( $i = 1-1.5d$ ); densely punctate ( $i < d$ ); crowded (interspaces sharp). Pubescence length is compared to the diameter of the median ocellus (MOD), and given as follows: minute ( $< 0.5 \times \text{MOD}$ ); short ( $= 0.5-1 \times \text{MOD}$ ); moderately short ( $= 1-1.5 \times \text{MOD}$ ); moderately long ( $= 1.5-2 \times \text{MOD}$ ); long ( $= 2-2.5 \times \text{MOD}$ ); very long ( $> 2.5 \times \text{MOD}$ ).

Body measurements were taken using a calibrated micrometer mounted on the stereomicroscope's ocular lens. Measurements were taken as follows: body length – sum of the metasomal length and the distance between the most produced part of the clypeus and the tip of the mesosoma in lateral view; head width – distance between the outer margins of the compound eyes in frontal view; head length – distance between the summit of the head and the lower margin of the clypeus in frontal view; intertegular distance – measured between the inner margins of the tegulae; forewing length – distance between the posterior margin of the tegula and the tip of the wing.

### *Images*

In this revision, I provide photographs of: (i) female and male (when known) of all recognized species, including the ones described herein; (ii) terminalia of all known males; (iii) characters used in the identification key. Photographs were taken with a Visionary Digital BK

Plus system, using a Canon 5D Mark II camera with a Canon 65mm lens. Image slices were amalgamated using Helicon Focus and final images were edited in Adobe Photoshop.

### *Species' distribution range*

In “Material studied” and “Range” sections, Chile’s major political regions are listed from north to south, in the following order: XV, I, II, III, IV, V, Metropolitana, VI, VII, VIII, IX, XVI, X, XI, XII. Until October 2007, what are now Regions XV and XIV were part of Regions I and X, respectively; therefore, any bee collected in Region XV or XIV before 2008 likely received what is currently an inaccurate locality label. All the examined specimens that fit this situation have been listed according to the current Chilean political regionalisation system.

The distribution range of the species are also given according to the biogeographic regionalisation of the Neotropical and Andean regions provided by Morrone (2014, 2015). Additionally, the northern Chilean (Regions XV, I and II) species are listed as occurring in either the summer or winter rainfall zones (or both), following Houston’s (2006) delineation (see Houston 2006: 2182). According to this author, in the southwest, most of the precipitation falls during the austral winter (May–July), whereas in the northeast the peak rainfall takes place in the austral summer (December–February).

Maps were created by plotting the distributions in QGIS v. 2.18.5 and then exporting pdf files for final edition in Adobe Illustrator CS5 v. 16.0.

### *Floral records*

Floral records for the species were obtained from the specimen’s labels and/or literature. The list of the new records (*i.e.* those reported for the first time in this study) is summarized in Table S2. The botanic classification adopted here is that of The Plant List’s website (The Plant List 2017).

## Results

### ***Colletes* Latreille, 1802**

Note: Synonymies presented for the genus are limited to those names applied to the Neotropical taxa (modified from Michener 1989).

*Colletes* Latreille, 1802: 423.

Type-species: *Apis succincta* Linnaeus, 1758.

*Monia* Westwood, 1875: 221 (junior homonym of *Monia* Gray, 1850).

Type-species: *Monia grisea* Westwood, 1875.

*Monidia* Cockerell, 1905: 9 (new name for *Monia* Westwood (not Gray)).

*Ptilopoda* Friese, 1921: 83.

Type-species: *Colletes (Ptilopoda) maculipennis* Friese, 1921 (junior synonym of *Colletes spiloptera* Cockerell, 1917a).

**Diagnosis:** Mid-sized, hairy, somewhat robust (males slightly slender) bees. Apex of glossa bilobed, compound eyes converging below at least in males, horizontal surface of metapostnotum limited posteriorly by carina (or sharp change in slope) and divided into pits by longitudinal carinae, posterior part of the second recurrent vein of forewing arcuate outwardly, basitibial and pygidial plates absent, prepygidial and pygidial fimbriae absent.

### **Species count**

This review contains 31 species, eight of them described as new. The occurrence of *C. neoqueenensis* Friese, 1910 in Chile, which has been acknowledged by a series of authors (e.g. Toro 1999; Montalva & Ruz 2010), could not be confirmed; therefore, this species is not formally treated here. Nevertheless, its female can be identified with the key provided at the end of this study.

***Colletes alocochila* Moure, 1956**

(Figs. 1A–F)

*Colletes alocochila* Moure, 1956: 208; Toro 1986: 122, 1999: 26; Moure & Urban 2002: 3; Moure *et al.* 2007: 678; Kuhlmann *et al.* 2009: 295; Montalva & Ruz 2010: 21; Ascher & Pickering 2017.

Holotype ♀ (examined). {DZUP}.

**Diagnosis:** The combination of labral median area depressed and margined by ridges, mesoscutal pubescence with off-white and black hairs intermixed, metasoma black and not covered with appressed hairs is sufficient to distinguish *C. alocochila* from all Chilean species, except the male of *C. murinus*. Male *C. alocochila* differs from that of *C. murinus* by its relatively longer F1, ~1.2x as long as its apical width (F1 as long as its apical width in *C. murinus*); and discs of T2–T5 without appressed hairs, with erect hairs only (discs of T2–T5 with appressed hairs intermingled with erect ones, in *C. murinus*).

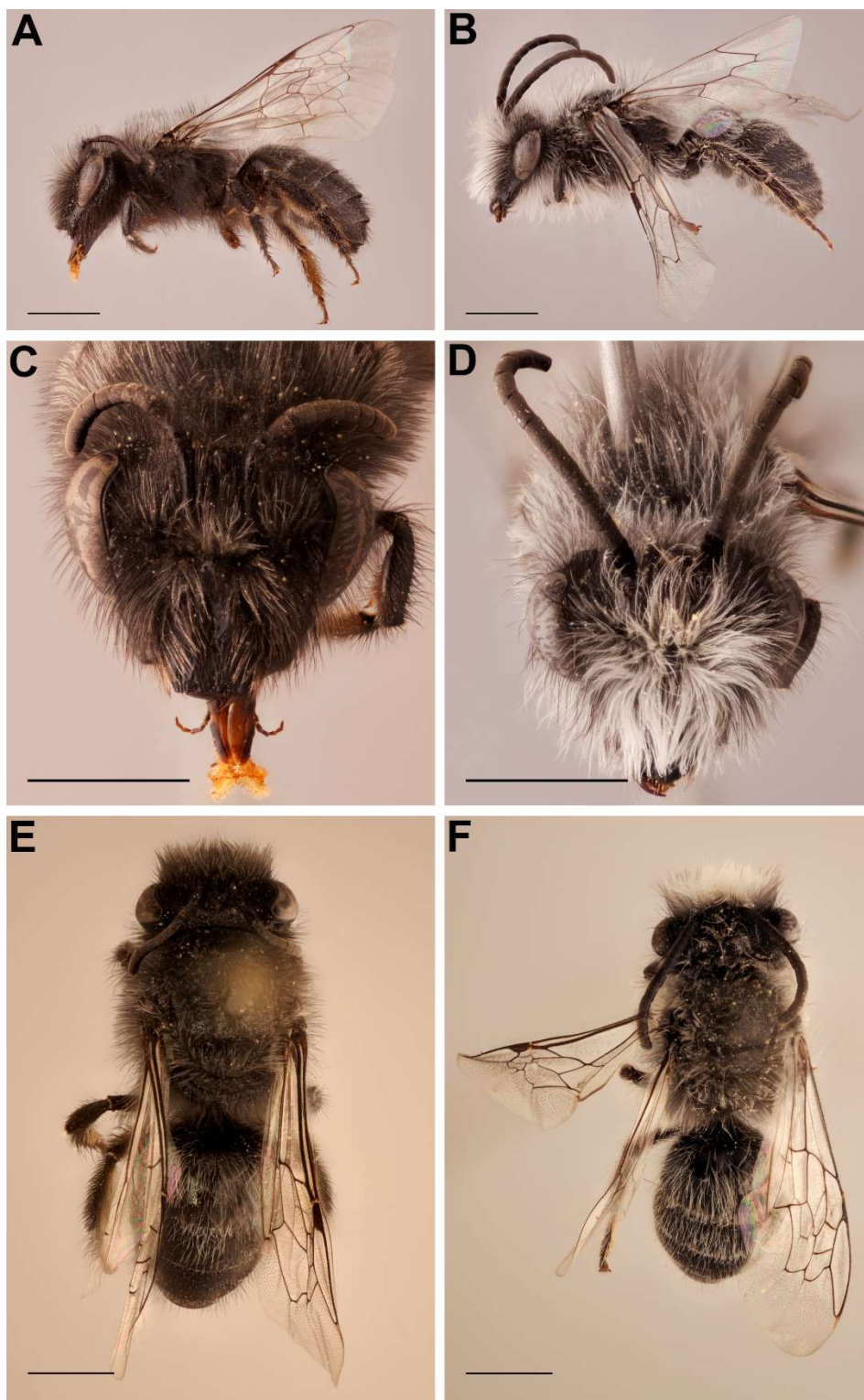
*Colletes alocochila* is very similar to two other species found in northern Chile, *C. nigropilosus* **n. sp.** and *C. mastochila*. However, it can be differentiated from the former by the mesoscutal anterior 1/3 only moderately densely punctate ( $i=d$ ) (mesoscutal anterior 1/3 comparatively more densely punctate ( $i<0.5d$ ) in *C. nigropilosus* **n. sp.**); and T1 with off-white pubescence (T1 with black pubescence in *C. nigropilosus* **n. sp.**). *Colletes alocochila* differs from *C. mastochila* in the following features: comparatively short body, about 9.5/9.0mm (♀/♂) in length (*C. mastochila* is about 12/11.5mm in length); and lateral surface of propodeum with rugulose interspaces (interspaces imbricate in *C. mastochila*).

**Redescription.** FEMALE (Figs. 1A, 1C, 1E):

*Dimensions (mm):* Approximate body length 9.2–10.1; head width 3.4–3.6; head length 2.7–2.8; intertegular distance 2.4–2.7; forewing length 7.6–8.1.

*Colouration:* Black except reddish-brown on distitarsi, distal half of tarsal claws; marked on distal 2/3 of mandible. Dark-brown on tegula, wing veins, stigma, marginal zones of metasomal terga and sterna. Dark-orange on proximal 1/3 of tarsal claws.





**Figure 1.** *Colletes alocochila* Moure, 1956. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area deeply and narrowly (0.4x MOD) depressed on upper half; depression progressively shallower towards lower margin; adjacent lateral area convex; apicomedial ridge absent. Malar area ~1.6x as long as basal depth of mandible (42:26). F1 ~1.3x as long as its apical width (57:42). UID:LID (76:72). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.6x as long as metanotum (23:40); metapostnotal pits well-delimited; posterior transverse carina straight and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3x longer than broad (64:21). Outer rami of hind tarsal claws 2x as long as inner rami (32:16). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Black, plumose, erect, long on lateral slopes of clypeus and supraclypeal area, lower paraocular and frontal areas, mesepisternum, metepisternum, ventral surface of coxae and trochanters, posteroventral surface of front femur, ventral margin of mid femur, S1; such hairs very long on vertexal area, upper margin of lateral surface of propodeum. Mixed black and off-white long hairs on upper paraocular and interantennal areas, mesoscutum, scutellum, metanotum. Black, erect, moderately long setae on mandible, posterior surfaces of front tibia and basitarsus, dorsal surface of mid tibia and basitarsus; such hairs very long on posterior margin of mid and hind basitarsi. Fulvous, suberect, moderately short setae on ventral surface of tarsi; such setae dark-orange and thick towards distal margin. Black, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T1 with off-white, plumose, erect, long hairs; such hairs only moderately long on T2. Disc of T3–T5 and S3–S6 with black, erect, moderately short setae; such setae long on T3–T5 laterally. Marginal zones of T1–T4 with off-white appressed hairs. S2 with black, suberect, long hairs, which are branched only apically.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and finely punctate; adjacent convex area with very sparse, moderately coarse punctures; lower 1/3 longitudinally striate. Malar area with moderately coarse and fine punctures intermingled; integument striate (except smooth near mandible and eye). Supraclypeal with very sparse moderately coarse punctures on disc (interspaces imbricate below, smooth above); crowded punctate on lateral slopes. Paraocular area punctures crowded and moderately fine; coarser towards upper clypeal margin. Frontal area punctures crowded. Vertexal area densely punctate; finely anteriorly;

coarser towards occipital area. Mesoscutum, scutellum and mesepisternum moderately coarsely and densely punctate (except sparsely punctate on disc of mesoscutum and anterior 1/6 of scutellum); interspaces smooth. Metanotum densely and moderately finely punctate; interspaces rugulose. Metepisternum obliquely striate medially; rugose above and below. Lateral surface of propodeum sparsely punctate; interspaces rugulose but somewhat shiny. Upper area of vertical surface of metapostnotum transversely striate medially. Metasomal terga with fine punctures intermingled with minute ones; T1 sparsely punctate; moderately densely punctate on remaining terga. Metasomal sterna finely punctate; densest on S2; sparsest on S6; interspaces imbricate throughout.

MALE (Figs. 1B, 1D, 1F). As in female, except for usual secondary sexual characteristics and as follows:

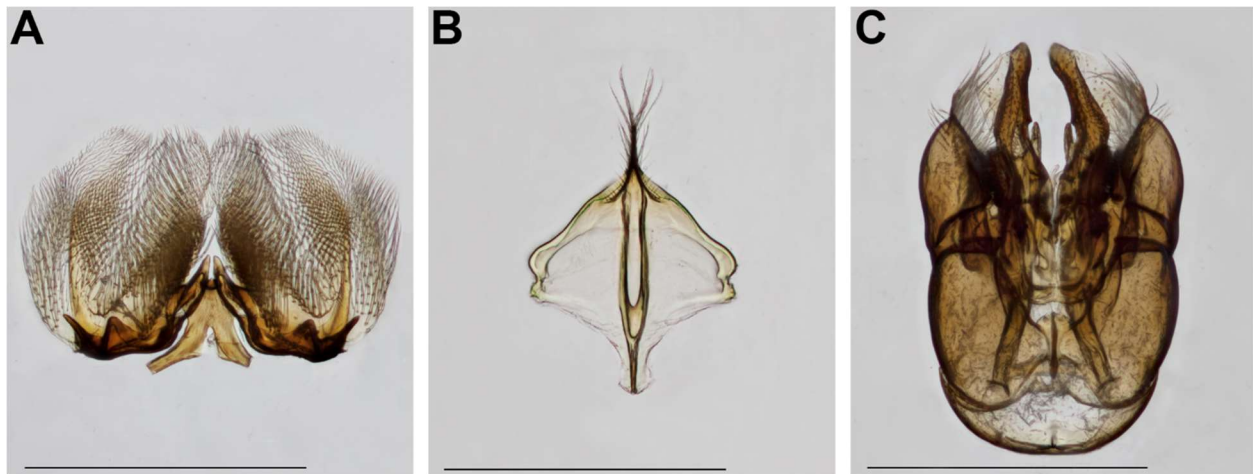
*Dimensions (mm)*: Approximate body length 8.6–9.3; head width 3.1–3.3; head length 2.7–2.9; intertegular distance 2.2–2.5; forewing length 7.2–7.6.

*Colouration*: Tegula blackish. Tibial spurs pale-orange. Marginal zones of S1–S5 dark-brown.

*Structure*: Clypeal mid-longitudinal depression slightly broader (0.5xMOD) on upper half. Malar area ~2x as long as basal depth of mandible (50:24). F1 ~1.2x as long as its apical width (45:38). UID:LID (97:82). Horizontal surface of metapostnotum ~0.35x as long as metanotum (23:68). Hind basitarsus ~3.5x longer than broad (82:24). Outer rami of hind tarsal claws ~2x as long as inner rami (26:14). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 2A, 2B, 2C, respectively.

*Pubescence*: Off-white on lateral slopes of clypeus and supraclypeal area, interantennal area, pronotal lobe, mesepisternum ventrally, legs (except ventral surface of tarsi pale-yellow), metasoma. Off-white and black hairs intermixed on genal area, mesoscutum, scutellum, metanotum.

*Surface sculpture*: Clypeal mid-longitudinal depression moderately coarsely punctate; convex area smooth throughout. Supraclypeal area densely and coarsely punctate; interspaces smooth and shiny throughout. Vertexal area punctures evenly crowded. Mesoscutum, scutellum and mesepisternum densely punctate. Metasomal terga evenly moderately finely punctate; T1 moderately densely punctate, T2-T5 densely punctate.



**Figure 2.** Dorsal view of the male terminalia of *C. alocochila*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** *Primary type specimen:* Holotype ♀ – “Antofagasta; S. Pedro Ataca.; 16.11.46”. “HOLOTIPO”. “Colletes ♀; alocochilus; P. Moure det 1948”. {DZUP}.

*Secondary type specimen:* Paratype ♀ – **CHILE – Region XV:** Putre, ii/1948, [G.Kuschel], 1 ♀, {DZUP}.

*Additional specimens:* **CHILE – Region XV:** 10km SE of Zapahuira, (-18.410, -69.537), 3435m, 8/iv/2000, [L.Packer], 2 ♀♀, {PCYU}. 50km S of Surire, (-19.362, -69.059), 4005m, 31/i/1998, [A.Ugarte], 1 ♂, {AMNH}. Belén, (-18.490, -69.527), 3231m, 21/x/1952, [L.Peña], 1 ♀, {KUNHM}; idem, except 25/x/1952, 1 ♀, {DZUP}. Coronel Alcerreca, (-17.995, -69.666), 3927m, 7/ii/1998, [A.Ugarte], 1 ♀, {AMNH}. Mirador de Socoroma, (-18.279, -69.584), 3414m, 7/iv/2000, [L.Packer], 1 ♀, {PCYU}. Putre, (-18.193, -69.578), 3433m, 16/xi/1997, [L.Packer], 1 ♀, {PCYU}; idem, except 4/iii/1984, [M.Kalin], 1 ♀, {KUNHM}. NE of Putre, (-18.180, -69.524), 4040m, 2/xi/2013, [S.Monckton], 3 ♀♀, {PCYU}. **Region I:** Chiu-Chiu, (-22.337, -68.615), 2555m, 24/i/1972, [L.Ruz], 1 ♀, {PUCV}. Chusmiza, (-19.682, -69.188), 3419m, 26/xi/2013, [Postlethwaite & Monckton], 1 ♀, {PCYU}. Highway 687 km 83, (-20.299, -69.057), 3843m, 4/xi/2013, [S.Monckton], 6 ♀♀2 ♂♂, {PCYU}; idem, except km 86, (-20.303, -69.039), 3983m, 1 ♀. **Region II:** 20km N of San Pedro de Atacama, (-22.731, -68.215), 2920m, 29/iii/2000, [L.Packer], 1 ♀, {PCYU}. 23km NW of San Pedro de Atacama, (-22.773, -68.371), 3210m, 15/x/2001, [Packer & Fraser], 1 ♂, {PCYU}. 29km E of San Pedro de Atacama, (-

22.930, -68.490), 2483m, 11/x/2001, [Packer & Fraser], 1♀, {PCYU}. 70km SE of Calama, (-22.665, -68.230), 3078m, [Postlethwaite & Monckton], 1♀, {PCYU}. Road to Machuca km 5, (-22.724, -68.054), 3511m, 27/x/2013, [S.Monckton], 1♂, {PCYU}. San Pedro de Atacama, (-22.910, -68.211), 2422m, iv/1952, [L.Peña], 1♀, {DZUP}; idem, except 20/ii/1960, 2♂♂, {AMNH}; idem, except 7/i/1971, 1♂, {PUCV}. **PERU – Puno:** Puno, (-15.847, -70.046), 4201m, iii/1935, 1♀, {DZUP}.

**Range:** Chile (Regions XV, I, II), Peru (Puno, Tacna). See also Fig. 3A.

**Biogeographic distribution:** South American transition zone: Desert, Puna and Atacama provinces. Northern Chilean and southern Peruvian species distributed in the summer rainfall area at altitudes of 2400–4300m a.s.l.

**DNA barcode:** Available. BOLD: ACW1920 (5♀♀3♂♂), BOLD: ACW1921 (1♀).

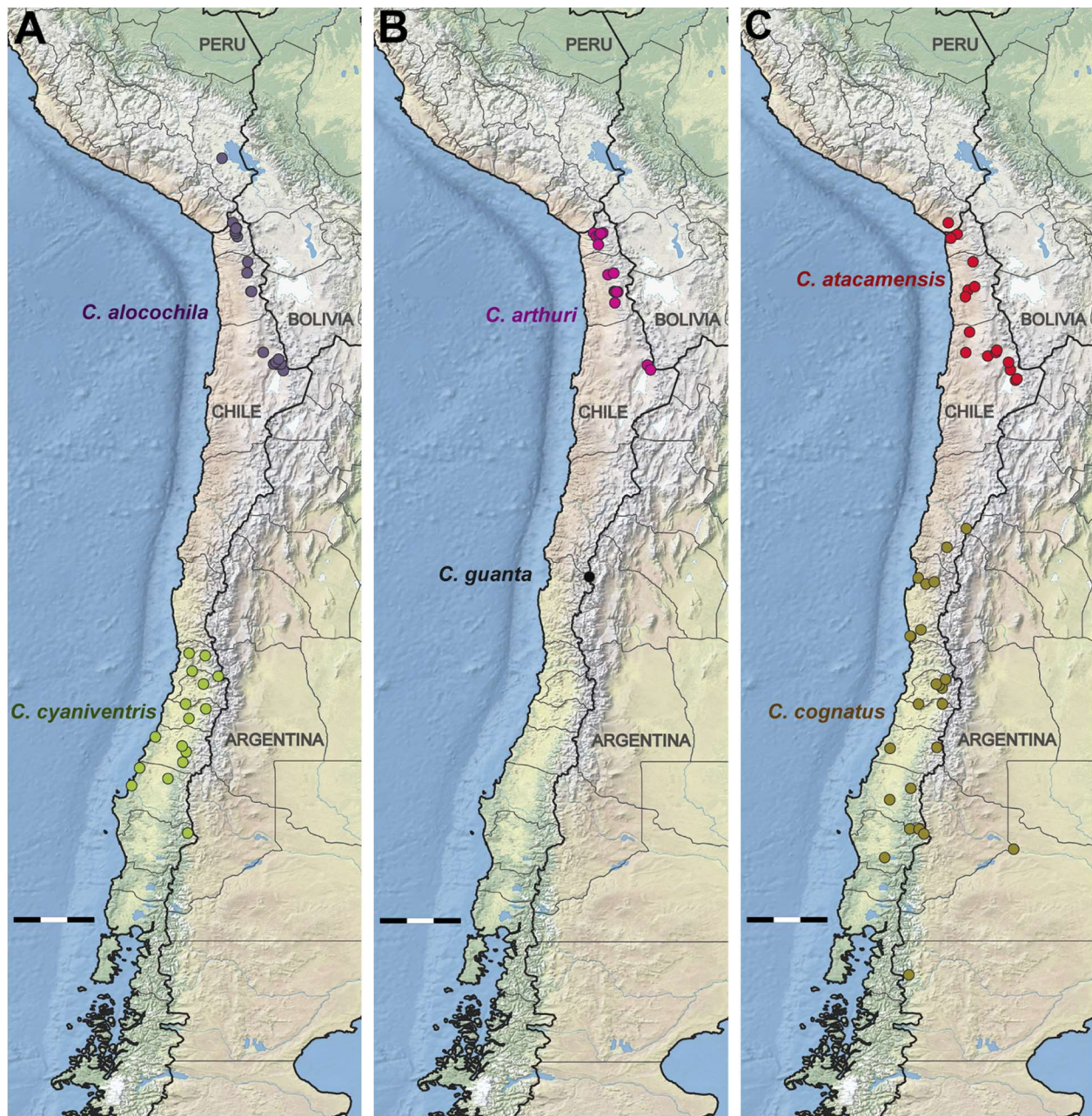
Representatives of both BINs occur sympatrically (see Table S1). Distance between BINs: 4.67–6.17%. Distance from the nearest neighbour (*C. nigropilosus* **n. sp.**): 8.59–9.62%.

**Floral hosts:** Leguminosae – *Medicago sativa* L. (Toro 1999).

**Comments:** In Chile, *C. alocochila* is only found at high altitudes in the northernmost regions, although the species is also distributed in southern Peru, also at high altitudes. As far as is known, a single floral record – *M. sativa* (Leguminosae) – is available for the species, but this is an introduced plant.

The type series of *C. alocochila* consists of four specimens: the female holotype, the male allotype, one male paratype, and one female paratype. The two males in this type series, however, actually belong to an undescribed species that is here being described as *C. nigropilosus* **n. sp.** (see below). Nevertheless, they must still be considered as valid paratypes of *C. alocochila*.





**Figure 3.** Geographic distribution by *Colletes* species. (A) *C. alocochila* and *C. cyaniventris*; (B) *C. arthuri* n. sp. and *C. guanta*; (C) *C. atacamensis* and *C. cognatus*. Scale bars approximately 300 km.

***Colletes arthuri* Ferrari, new species**

(Figs. 4A–F)

**Diagnosis:** *Colletes arthuri* **n. sp.** is recognizable by the combination of pubescence almost entirely pale-yellow, and upper area of vertical surface of metapostnotum projected posteriorly in relation to horizontal surface (or upper area of vertical surface convex, when seen in lateral view).

*Colletes arthuri* **n. sp.** is most similar to *C. cognatus*, but the female of the former is distinct in having the discs of T2–T5 covered with dense appressed hairs (discs of T2–T5 without appressed hairs in female *C. cognatus*). The males can be distinguished from one another by the comparatively long malar area, ~2x as long as basal depth of mandible, in *C. arthuri* **n. sp.** (malar area ~1.5x as long as basal depth of mandible in the male *C. cognatus*); and by mesepisternum with only moderately coarsely punctate in *C. arthuri* **n. sp.** (mesepisternum with coarse and minute punctures intermingled in male *C. cognatus*).

**Description:** FEMALE (Figs. 4A, 4C, 4E):

*Dimensions (mm):* Approximate body length 9.4; head width 2.8; head length 2.3; intertegular distance 2.2; forewing length 7.0.

*Colouration:* Black except dark-brown on tegula, forewing veins (except proximal 1/3 of veins M+Cu and V pale-brown), tarsomeres 2–5 (except mid-longitudinal band of distitarsi pale-brown), ventral surface and marginal zone of T1, discs of T5–T6, distal 1/5 of S2–S5. Pale-brown on stigma, hindwing veins, proximal half of tarsal claws, marginal zones of T2–T4, mid-longitudinal band of S2, distal 1/4 of S6. Reddish-brown on distal half of tarsal claws; marked on distal 1/3 of mandible. Pale-yellow on tibial spurs, marginal zones of metasomal sterna.

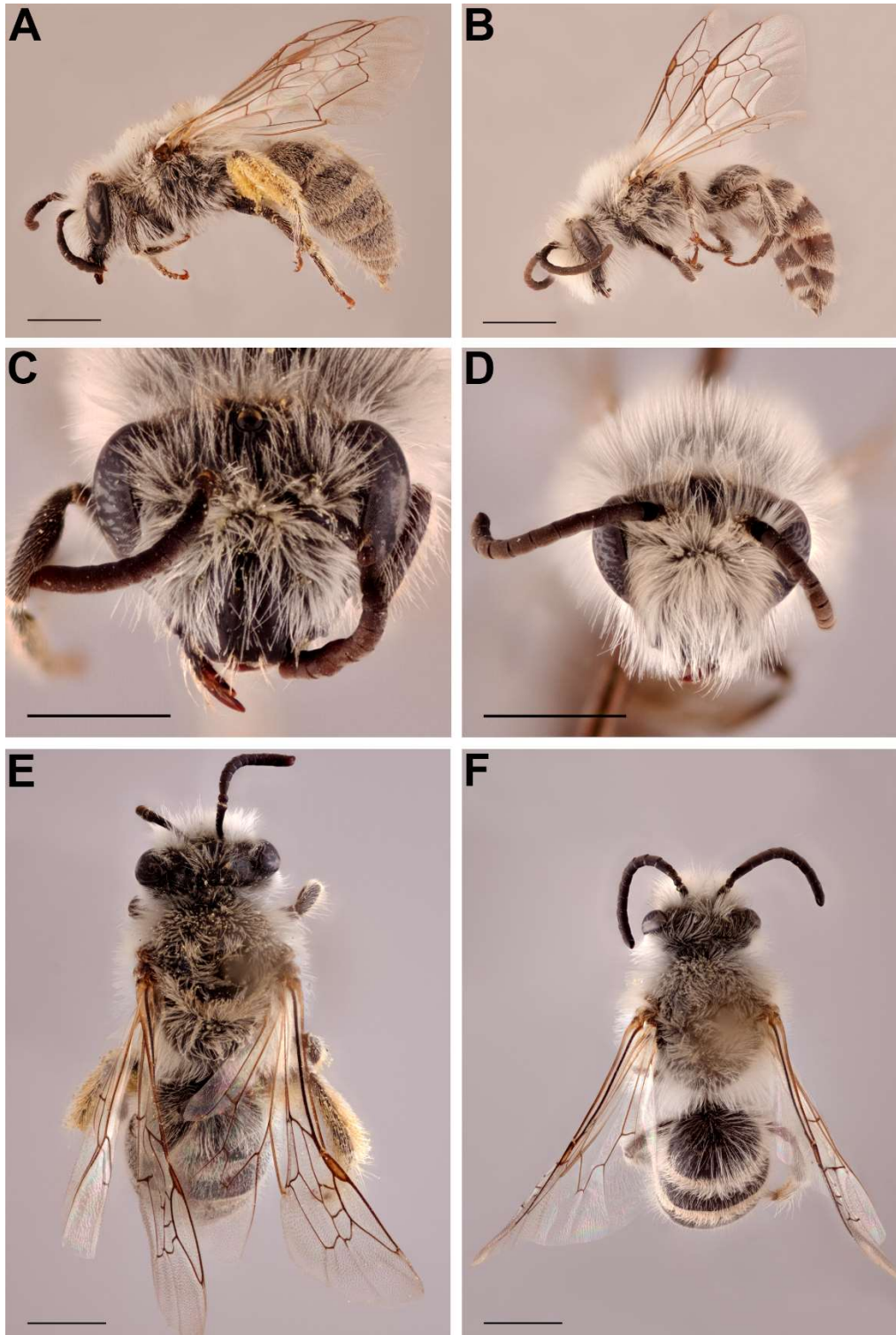
*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area evenly shallowly depressed; depression narrow (0.6x MOD) for upper 3/5; broad (1.7x MOD) on lower 2/5; adjacent lateral area convex; apicomedial ridge absent. Malar area ~1.3x as long as basal depth of mandible (37:39). F1 ~1.3x as long as its apical width (30:29). UID:LID (62:56). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded. Horizontal surface of metapostnotum about half as long as metanotum (23:51); metapostnotal pits poorly-delimited; posterior transverse carina

difficult to discern from the other carinae on upper area of vertical surface of propodeum. Posteromedial surface of front coxa without spine. Posterior hind tibial spur pectinate. Hind basitarsus ~3.8x longer than broad (49:13). Outer rami of hind tarsal claws 1.5x as long as inner rami (15:10). Posterolateral area of S6 flat and lacking carina; marginal zone not depressed.

*Pubescence:* Pale-yellow, plumose, erect, moderately long on clypeus (except suberect mid-longitudinally), lateral slopes of supraclypeal area, ventral surface of mid and hind trochanters, ventral margin of mid femur, S1; such hairs long on interantennal and vertexal areas, scutellum, mesepisternum, metepisternum, posteroventral of front trochanter and femur, T1; very long on upper margin of lateral surface propodeum; pale-yellow hairs intermingled with black ones on frontal and vertexal areas, mesoscutum, scutellum. Pale-yellow, erect, moderately short setae on mandible, dorsal surface of mid and hind basitarsi and hind tibia; moderately long on posterior surface of front tibia and basitarsus, posterior margin of mid basitarsus; very long on posterior margin of hind basitarsus. Bright-yellow, suberect, thick setae on ventral surface of mid and hind tarsi; pale-orange, thickest towards distal margin. Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T1–T5 covered with dense, pale-yellow appressed hairs; T2 also with plumose, erect short hairs; T3–T5 also with fulvous and pale-yellow, erect, moderately short setae (except short on T3). S2 with pale-yellow, erect, moderately short hairs, which are branched only apically. Discs of S3–S6 covered with pale-yellow, suberect, minute setae (except short on S6); marginal zones of S2–S5 with plumose hairs.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and moderately finely punctate; adjacent convex area with very sparse punctures; interspaces smooth and shiny (except longitudinally striate on lower 1/5). Malar area sparsely and finely punctate on upper 1/3 (interspaces smooth); densely and moderately finely punctate on lower 2/3 (interspaces rugulose). Supraclypeal area largely impunctate and smooth (except with few punctures on lower and lateral margins). Paraocular area densely punctate; moderately finely punctate below; finely punctate above; interspaces smooth throughout. Frontal area densely and moderately coarsely punctate; interspaces smooth. Vertexal area sparsely and minutely punctate; interspaces smooth and shiny. Mesosomal interspaces smooth throughout (except when stated otherwise). Mesoscutum and scutellum moderately densely and moderately finely punctate (except sparsely punctate on mesoscutal mid-posterior area and densely punctate on scutellar posterior 1/4).





**Figure 4.** *Colletes arthuri* Ferrari, n. sp. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

Metanotum densely and moderately finely punctate. Mesepisternum densely and coarsely punctate (except slightly finer anteriorly to episternal groove). Metepisternum rugose above; rugulose medially and below. Lateral surface of propodeum with very sparse fine punctures difficult to discern from the rugulose integument. Upper area of vertical surface of metapostnotum transversely striate. Metasomal terga minutely punctate; T1 sparsely punctate; T2–T5 moderately densely punctate; interspaces smooth throughout. Metasomal sterna finely punctate; S2–S3 sparsely punctate; denser on S4; densest on S5; S6 with a few moderately fine punctures on posterior half; interspaces imbricate throughout.

MALE (Figs. 4B, 4D, 4F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 8.2; head width 2.8; head length 2.2; intertegular distance 2.1; forewing length 7.1.

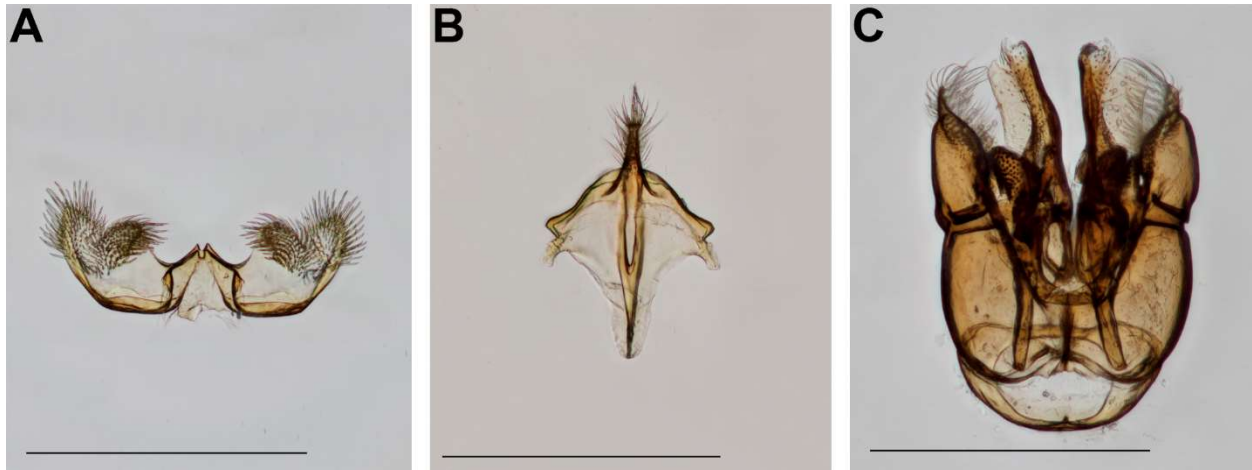
*Colouration*: Hindwing veins and marginal zones of T5–T6 pale-brown. Ventrally reflexed lateral areas of T1 black. S2 and S6 evenly black.

*Structure*: Labral median depression not margined by ridges. Clypeal mid-longitudinal area evenly moderately broadly (0.6x MOD) depressed. Malar area ~2x as long as basal depth of mandible (42:22). F1 ~0.8x as long as its apical width (24:29). UID:LID (63:55). Horizontal surface of metapostnotum about half as long as metanotum (23:51). Posterior hind tibial spur ciliate. Hind basitarsus ~4x longer than broad (39:10). Outer rami of hind tarsal claws 1.5x as long as inner rami (12:8). S7, S8 and genital capsule as in Figs. 5A, 5B, 5C, respectively.

*Pubescence*: Pale-yellow hairs on paraocular area intermingled with black ones. Mesoscutal and scutellar pubescence entirely pale-yellow. Appressed hairs on T1–T2 restricted to marginal zones; on T3, scattered on disc. Plumose hairs on T2 moderately long. S2 with plumose hairs only. Marginal bands of S2–S5 moderately short.

*Surface sculpture*: Clypeal mid-longitudinal depression finely punctate; lower margin smooth. Supraclypeal area densely and moderately finely punctate. Vertexal area with minute punctures intermingled with moderately fine ones. Scutellum sparsely punctate. Mesepisternum moderately coarsely punctate. Metasomal terga finely punctate; T1 moderately sparsely punctate; T3–T5 with rugulose interspaces. S6 finely punctate.





**Figure 5.** Dorsal view of the male terminalia of *C. arthuri* n. sp. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Type material:** *Holotype* ♀ – “CHILE, Region I, 79.8 km; ESE of; Pozo Almonte; 8-21.ix.2004; L. Packer”. “Packer Coll.; York Univ.; 0014430”. “HOLOTYPE; *Colletes arthuri* ♀; Ferrari, new species”. {PCYU}.

**Paratypes:** **CHILE – Region XV:** 30km W of Zapahuira, (-18.333, -69.894), 1799m, 3/iv/2000, [L.Packer], 2♂♂, {PCYU}. Quebrada Cardones, (-18.456, -69.772), 2435m, 13/v/2012, [L.Packer], 1♂, {PCYU}. S of Putre, (-18.413, -69.669), 3046m, 3/ii/2013, [Postlethwaite & Monckton], 2♀♀3♂♂, {PCYU}. SW of Tignamar, (-18.726, -69.702), 2509m, 31/i/2013, [Postlethwaite & Monckton], 1♀, {PCYU}. Tambo, (-18.356, -69.620), 3235m, 12/iv/2004, [L.Packer], 1♂, {PCYU}. **Region I:** 20km W of Chusmiza, (-19.711, -69.420), 2211m, 11/iv/2000, [L.Packer], 1♀1♂, {PCYU}. 68km SE of Pozo Almonte, (-18.333, -69.552), 3803m, 8/iv/2004, [L.Packer], 1♀, {PCYU}. 69km E of Pozo Almonte, (-20.291, -69.168), 2821m, 16/iv/2012, [L.Packer], 6♀♀2♂♂, {PCYU}. 71km E of Pozo Almonte, (-20.297, -69.142), 3052m, 14/iv/2012, [L.Packer], 16♀♀6♂♂, {PCYU}; idem, except 16/iv/2012, 1♀; idem, except 10/v/2012, 18♀♀33♂♂. 72.5km ESE of Pozo Almonte, (-20.300, -69.116), 3341m, [L.Packer], 3♀♀, {PCYU}; idem, except 9/iv/2004, 2♀♀1♂. 73km E of Pozo Almonte, (-20.312, -69.129), 3188m, 21/iv/2012, [L.Packer], 10♀♀40♂♂, {PCYU}; idem, except 16/iv/2012, 8♀♀12♂♂; idem, except 10/v/2012, 1♀1♂♂; idem, except 16/v/2012, 1♀3♂♂. 79.8km ESE of Pozo Almonte, (-20.313, -69.041), 4061m, 8/iv/2004, [L.Packer], 7♀♀51♂♂,

{PCYU}; idem, except 8/ix/2004, 1♀28♂♂. 83.5km ESE of Pozo Almonte, (-20.305, -69.053), 3886m, 8/iv/2004, [L.Packer], 1♀3♂♂, {PCYU}. Chusmiza, (-19.682, -69.188), 3419m, 11/iv/2004, [L.Packer], 1♀1♂, {PCYU}. E of Pozo Almonte, (-20.298, -69.141), 3064m, 6/ii/2013, [Postlethwaite & Monckton], 5♀♀5♂♂, {PCYU}; idem, except 9/iv/2013, 2♀♀3♂♂. W of Pozo Almonte, (-20.302, -69.094), 3545m, 11/iv/2013, [Postlethwaite & Monckton], 1♀1♂, {PCYU}. **Region II:** 5–7km E of Aguas Blancas, (-23.329, -67.950), 2762m, 7/iv/2004, [L.Packer], 2♀♀1♂, {PCYU}. Gautin, (-22.750, -68.066), 3304m, iv/2004, [L.Packer], 1♀, {PCYU}. Highway CH-27 km 24, (-22.908, -67.962), 3357m, [L.Packer], 1♂, {PCYU}; idem, except km 25.9, (-22.910, -67.943), 3491m, [Postlethwaite & Monckton], 1♂.

**Range:** Chile (Regions XV, I, II). See also Fig. 3B.

**Biogeographic distribution:** South American transition zone: Desert and Atacama provinces. Northern Chilean species distributed in the summer rainfall area at altitudes of 1700–4100m a.s.l.

**DNA barcode:** Available. BOLD: AAN4840 (8♀♀5♂♂). Distance from the nearest neighbour (*C. cyanescens*): 9.02–9.52%.

**Floral hosts:** Unknown.

**Etymology:** Species named after my beloved son, Arthur Ferrari.

**Comments:** *Colletes arthuri* n. sp. was the most abundant species amongst the hundreds of *Colletes* specimens obtained via pan traps by L. Packer and colleagues in northern Chile, especially Region I. However, I examined no bee that has been collected with hand net while visiting flowers, which is why no floral host for the species is known.

***Colletes atacamensis* Janvier, 1955**

(Figs. 6A–F)

*Colletes atacamensis* Janvier, 1955: 316; Toro 1986: 122; 1999: 26; Moure & Urban 2002: 4; Moure *et al.* 2007: 678; Kuhlmann *et al.* 2009: 296; Montalva & Ruz 2010: 21; Ascher & Pickering 2017.

Syntypes ♀ and ♂ (not examined). {whereabouts unknown}.

*Colletes atacamensis* Moure, 1956: 204 (junior homonym of *Colletes atacamensis* Janvier, 1955).

Holotype ♀ (examined). {DZUP}.

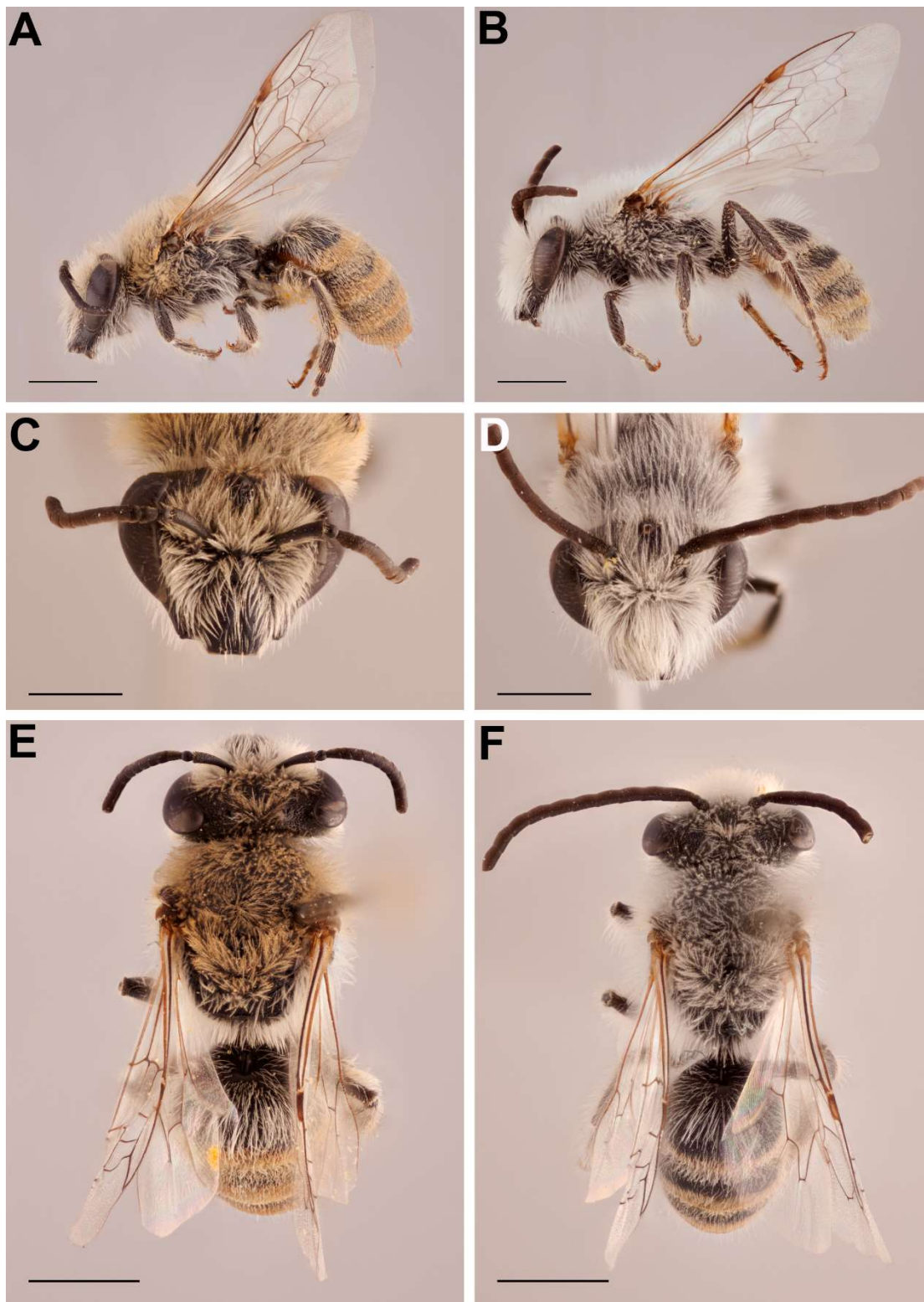
*Colletes atacamanus* Moure, 1997: 513 [new name for *Colletes atacamensis* Moure (not Janvier)]; Moure & Urban 2002: 4; Moure *et al.* 2007: 678. Synonymy proposed by Toro (1999: 26).

**Diagnosis:** *Colletes atacamensis* is easily recognizable due to the remarkably coarse punctation on T1 (coarser than that on mesepisternum), which differentiates it from all other species of the genus found in Chile, except the male *C. simulatus* **n. sp.** However, the males of these species can be distinguished from each other by the absence of black hairs on the paraocular area and mesosomal dorsum in *C. atacamensis* (pubescence on paraocular area and mesosomal dorsum with off-white and black hairs intermixed in *C. simulatus* **n. sp.**); and mesoscutum moderately densely punctate ( $i=1-1.5d$ ) in *C. atacamensis* (mesoscutum densely punctate ( $i=0.5d$ ) in *C. simulatus* **n. sp.**).

**Redescription:** FEMALE (Figs. 6A, 6C, 6E):

*Dimensions (mm):* Approximate body length 7.5–7.9; head width 2.8–2.9; head length 2.2–2.3; intertegular distance 1.9–2.2; forewing length 6.5–6.9.

*Colouration:* Black except pale-yellow on tibial spurs, marginal zones of T1–T5 and S1–S5. Reddish-brown on distal half of tarsal claws; marked on distal 1/3 of mandible. Dark-brown on wing veins, distitarsi (except distal 1/5 pale-brown). Pale-brown on stigma, proximal half of tarsal claws.



**Figure 6.** *Colletes atacamensis* Janvier, 1955. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area evenly shallowly and narrowly (0.3x MOD) depressed; adjacent lateral area convex; apicomedial ridge absent. Malar area  $\sim 1.3x$  as long as basal depth of mandible (30:23). F1  $\sim 1.1x$  as long as its apical width (39:36). UID:LID (58:54). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum  $\sim 0.9x$  as long as metanotum (52:58); metapostnotal pits poorly-delimited; posterior transverse carina straight and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 3.7x$  longer than broad (48:13). Outer rami of hind tarsal claws  $\sim 2.8x$  as long as inner rami (40:14). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Pale-yellow, plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, paraocular and interantennal areas, frontal area, mesoscutum, scutellum, posteroventral surface of front trochanter and femur, ventral surface of mid and hind coxae, ventral margin of mid femur, S1; such hairs long on vertexal and genal areas (except moderately short behind eye), metanotum, mesepisternum, metepisternum, ventral surface of mid and hind trochanters, T1; very long on upper margin of lateral surface of propodeum. Bright-yellow, suberect, moderately short setae on dorsal surface of front and mid tibiae; such hairs erect, moderately long on mandible, dorsal surface of mid and hind tibiae and basitarsi; very long on posterior margin of mid and hind tarsi. Bright-yellow, suberect, thick setae on ventral surface of mid and hind tarsi; bright-orange, thickest towards distal margin. Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. Pale-yellow, dense appressed hairs on T1 laterally and T2–T5. S2 with pale-yellow, erect, moderately short hairs, which are branched only apically. S3–S6 with moderately short, erect setae; plumose, suberect hairs on marginal zones (except S6).

*Surface sculpture:* Clypeus shiny throughout; mid-longitudinal depression densely and moderately finely punctate; adjacent convex area largely impunctate. Malar area longitudinally striate. Supraclypeal area with very sparse coarse punctures (except densely punctate on lateral slopes); interspaces smooth and shiny. Paraocular area densely and moderately finely punctate (except punctures crowded near malar area). Frontal area densely and moderately coarsely punctate; interspaces rugulose. Vertexal area punctures crowded and moderately coarse; sparser and finer towards compound eye. Mesoscutum, scutellum and mesepisternum moderately



sparsely and moderately coarsely punctate (except sparsely punctate on scutellar anterior 1/3); interspaces smooth and shiny. Metanotum densely and moderately coarsely punctate; interspaces rugulose but somewhat shiny. Metepisternum rugulose above and below; obliquely striate medially. Lateral surface of propodeum densely and moderately coarsely punctate on upper 1/4; sparsely and coarsely punctate on lower 3/4; interspaces rugulose but somewhat shiny. Upper area of vertical surface of metapostnotum rugose medially. Metasomal terga densely punctate; strongly coarsely punctate on T1; punctures progressively finer towards T5; interspaces smooth and shiny throughout. Metasomal sterna moderately sparsely and moderately finely punctate; interspaces imbricate.

MALE (Figs. 6B, 6D, 6F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 6.9–7.4; head width 2.6–2.8; head length 2.1–2.2; intertegular distance 1.5–1.8; forewing length 6.1–6.4.

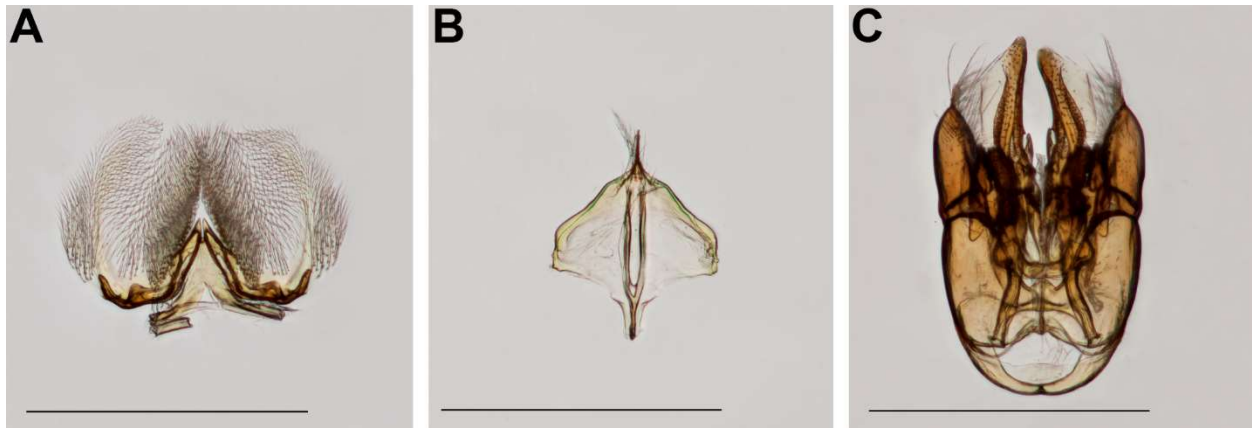
*Colouration*: Tegula dark-brown. Wing veins pale-brown (except vein R of forewing dark-brown).

*Structure*: Malar area 2x as long as basal depth of mandible (38:19). F1 ~0.9x as long as its apical width (42:45). UID:LID (60:48). Horizontal surface of metapostnotum ~0.8x as long as metanotum (34:44); metapostnotal pits well-delimited; posterior transverse carina sinuous. Hind basitarsus ~4.1x longer than broad (49:12). Outer rami of hind tarsal claws ~1.3x as long as inner rami (24:18). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 7A, 7B, 7C, respectively.

*Pubescence*: Off-white throughout. Mesoscutum and scutellum with long hairs. Dorsal surface of mid and hind basitarsi with long setae. S2 with plumose hairs only. Plumose hairs on marginal zones of S3–S6 erect.

*Surface sculpture*: Frontal and vertexal areas punctures crowded throughout. Lateral surface of propodeum with rugose interspaces. Metasomal sterna finely punctate.

**Material studied:** *Primary type specimen*: Holotype ♀ of *C. atacamensis* Moure (not Janvier) – “S. Pedro; 16-xi-46; Atacama”. “HOLOTIPO”. “Colletes ♀; atacamensis; P. Moure det 1948”. {DZUP}.



**Figure 7.** Dorsal view of the male terminalia of *C. atacamensis*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Secondary type specimens:* Paratypes ♀♀ and ♂♂ of *C. atacamensis* Moure (not Janvier)  
– **CHILE – Region II:** San Pedro de Atacama, 16/xi/1946, [G.Kuschel], 5♀♀3♂♂, {DZUP}.

*Additional specimens:* **CHILE – Region XV:** Arica, (-18.486, -70.317), 120m, 1♂, {MHNP}. San Miguel Azapa, (-18.520, -70.160), 346m, 29/x/2000, [L.Packer], 1♂, {PCYU}; idem, except iii/1995, [Arriagada], 1♂, {AMNH}. Mollinos, (-18.383, -69.945), 1005m, 14/ii/1993, [L.Peña], 1♀, {AMNH}. Quebrada Azapa, (-18.519, -70.155), 432m, ix/1968, [D.Hoz], 1♀, {AMNH}. Yala-yala, (-19.310, -69.419), 2460m, 11/iv/2004, [L.Packer], 2♀♀, {PCYU}. **Region I:** 22km E of Pozo Almonte, (-20.251, -69.580), 1057m, 22/ix/2013, [Almeida & Packer], 6♂♂, {RPSP}. 23km E of Pozo Almonte, (-20.251, -69.555), 1081m, 22/ix/2013, [Almeida & Packer], 4♀♀13♂♂, {RPSP}. E of Pozo Almonte, (-20.252, -69.581), 1057m, 6/ii/2013, [Postlethwaite & Monckton], 4♂♂, {PCYU}; idem, except 9/iv/2004, [L.Packer], 2♀♀3♂♂; idem, except 17/iv/2004, [L.Packer], 1♀. Highway 687 km 7.8, (-20.252, -69.581), 1056m, 4/xi/2013, [S.Monckton], 1♀, {PCYU}. Parque Nacional Pampa del Tamarugal, (-20.474, -69.684), 990m, 26/x/2000, [L.Packer], 2♂♂, {PCYU}. Pozo Almonte, (-20.141, -69.363), 2013m, 27/ix/2013, [L.Packer], 1♂, {PCYU}. **Region II:** 5km S of Toconao, (-23.267, -67.997), 2457m, 25/iii/2000, [L.Packer], 1♀, {PCYU}. 32km of Toconao, 12/x/2001, [Packer & Fraser], 1♂, {PCYU}. Aguas Verdes, i/1992, [H.Toro], 1♀, {PUCV}. Calama, (-22.428, -68.917), 2303m, ii/1992, [L.Peña], 1♂, {AMNH}. Chiu-Chiu, (-22.337, -68.615), 2555m, 30/iii/2000, [L.Packer], 1♀3♂♂, {PCYU}. Lasana, (-22.266, -68.621), 2701m, xi/1996,

[U.Peña], 8♂♂, {AMNH}. Maria Elena, (-22.342, -69.644), 1269m, 14/xi/1997, [L.Packer], 1♂, {PCYU}. Quillagua, (-21.663, -69.529), 848m, x/1966, [L.Peña], 1♂, {AMNH}; idem, except x/1969, [H.Toro], 1♂. San Pedro de Atacama, (-22.923, -68.166), 2426m, 22/xi/2002, [Grixti & Zayed], 2♀♀, {PCYU}; idem, except 7/i/1971, [W.Sielfeld], 1♂, {AMNH}; idem, except 20/ii/1960, [L.Peña], 4♀♀, {AMNH}; idem, except 16/xi/1946, 1♀, {KUNHM}. W of Rio Grande, (-22.665, -68.230), 3078m, 21/x/2013, [Postlethwaite & Monckton], 1♀2♂♂, {PCYU}. **PERU – Tacna:** Tacna, (-17.998, -70.273), 763m, 13/xi/1955, [L.Peña], 1♂, {KUNHM}.

**Range:** Chile (Regions XV, I, II), Peru (Tacna). See also Fig. 3C.

**Biogeographic distribution:** South American transition zone: Desert and Atacama provinces. Northern Chilean and southern Peruvian species distributed in both summer and winter rainfall areas, at altitudes of 100–3100m a.s.l.

**DNA barcode:** Available. BOLD: AAJ6725 (3♀♀6♂♂). Distance from the nearest neighbour (*C. fulvipes*): 9.06–9.34%.

**Floral hosts:** Leguminosae – *Caesalpinia* sp. (this study); *Medicago sativa* L. (Toro 1999); *Prosopis alba* Griseb. (Toro 1999); *P. tamarugo* Phil. (Toro 1999).

**Comments:** Although *C. atacamensis* has a comparatively limited geographic distribution in Chile (Regions XV–II, but also found in the Peruvian region of Tacna), the species is relatively common in most of its range.

Several attempts to locate the female and male syntypes of *C. atacamensis* Janvier at the MNHP, where these type specimens were speculated to be deposited (Moure & Urban 2002: 4), were unsuccessful (A. Touret-Alby, *pers. comm.*). Thus, final decision on its identity was made based on the original description, and by comparison with specimens previously identified by H. Toro, who synonymized *C. atacamanus* under *C. atacamensis* Janvier (Toro 1999: 26).

***Colletes atripes* Smith, 1854**

(Figs. 8A–F)

*Colletes dimidiata* Spinola, 1851: 225 (junior homonym of *Colletes dimidiata* Brullé, 1840).

Lectotype ♀ (not examined) designated by Moure & Urban (2002: 4). {MRSN}.

*Colletes atripes* Smith, 1854: 418 [new name for *Colletes dimidiata* Spinola (not Brullé)]; Dalla Torre 1896: 37; Jafuel & Pirion 1926: 364; Toro 1986: 122, 1999: 26; Moure & Urban 2002: 4; Moure *et al.* 2007: 678; Kuhlmann *et al.* 2009: 296; Montalva & Ruz 2010: 21; Ascher & Pickering 2017.

**Diagnosis:** The combination of mesosomal dorsum and T1 with ferruginous pubescence, metasoma black, and marginal zones of metasomal terga not covered with appressed hairs is sufficient to distinguish *C. atripes* from all congeneric species found in Chile.

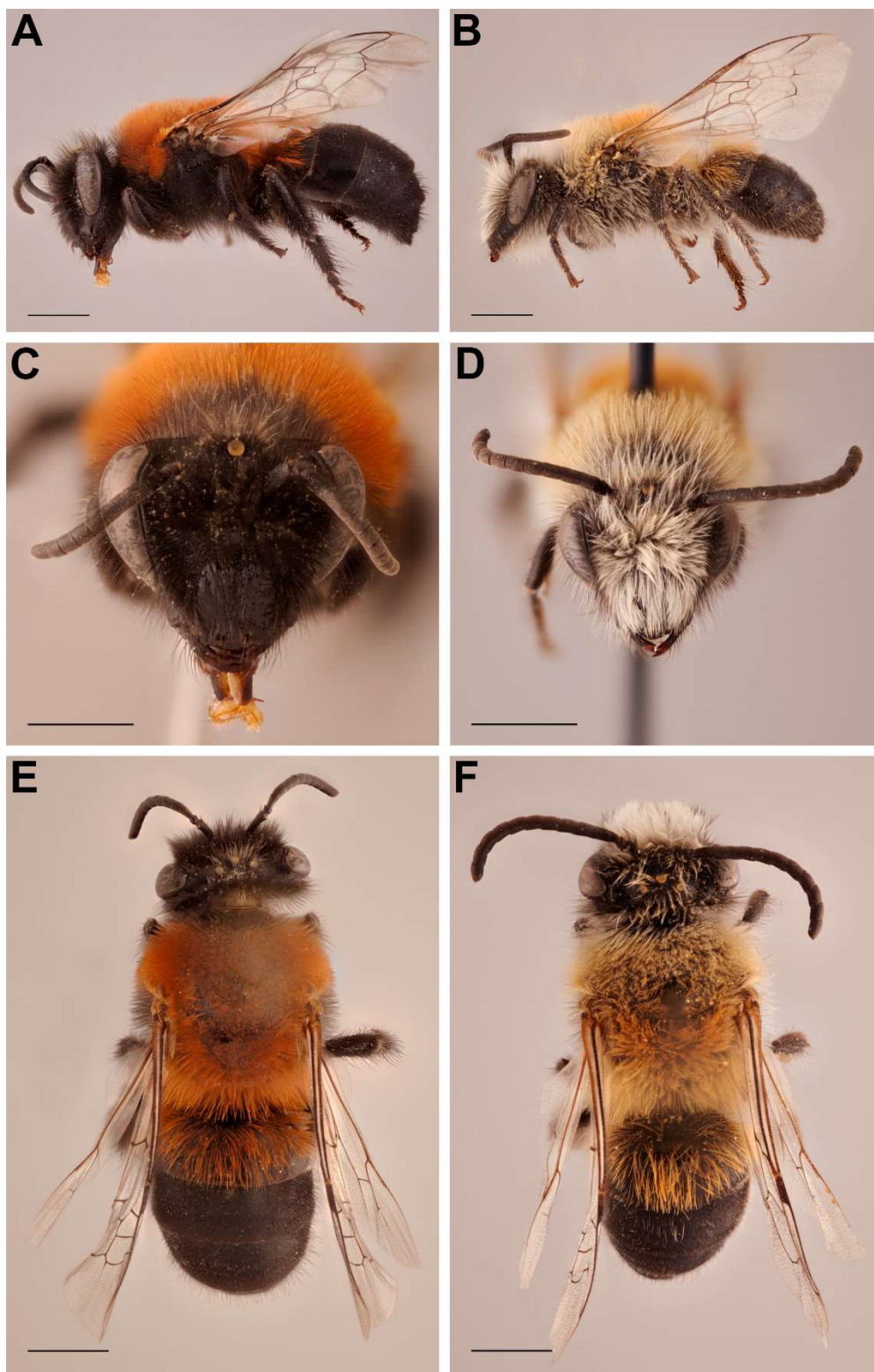
*Colletes atripes* is similar to *C. bicolor*, *C. flaminii*, and *C. fulvipes*, from which it can be differentiated by the dull, black metasoma (the other three species have a metallic blue metasoma).

**Redescription:** FEMALE (Figs. 8A, 8C, 8E):

*Dimensions (mm):* Approximate body length 10.8–11.9; head width 3.5–3.9; head length 2.8–3.0; intertegular distance 3.2–3.5; forewing length 7.5–8.2.

*Colouration:* Black except reddish-brown on distal 2/3 of tarsal claws; marked on distal half of mandible. Pale-orange on tegula, proximal 1/3 of tarsal claws. Pale-brown on ventrally reflexed lateral areas of T1–T2. Dark-brown on tibial spurs, anterior surface of front and mid femora, ventral surface of hind femur, tarsi (except basitarsi black), wing veins (except vein R of forewing black), marginal zone of T1, disc of S6.

*Structure:* Labrum medially convex; convexity not margined by ridges. Clypeal mid-longitudinal area neither depressed nor carinate; adjacent lateral area convex; apicomedial ridge present. Malar area ~1.2x as long as basal depth of mandible (38:32). F1 ~1.3x as long as its apical width (48:36). UID:LID (70:63). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute.



**Figure 8.** *Colletes atripes* Smith, 1854. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.



Horizontal surface of metapostnotum  $\sim 0.35x$  as long as metanotum (22:60); metapostnotal pits well-delimited; posterior transverse carina sinuous and narrowly interrupted medially.

Posteromedial surface of front coxa bearing long spine ( $0.65x$  MOD). Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 3.2x$  longer than broad (52:16). Outer rami of hind tarsal claws  $\sim 1.8x$  as long as inner rami (37:20). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Black, plumose, erect, long on lateral slopes of clypeus and supraclypeal area, interantennal, paraocular, frontal, vertexal and genal areas, mesepisternum, metepisternum, posteroventral surface of front femur; such hairs moderately long on ventral surface of mid and hind coxae and trochanters, ventral margin of mid femur, S1. Ferruginous, plumose, erect, moderately long on pronotal lobe, mesoscutum, scutellum; such hairs long on metanotum, T1 (except suberect, moderately long laterally); very long on upper margin of lateral surface of propodeum. Lateral surface of propodeum with off-white, sparse appressed hairs. Black, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia; such hairs erect, moderately long on ventral surface of hind coxa and trochanter. Fulvous, suberect, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Black, erect, short setae on discs of T2–T3; moderately short on T3 laterally, discs of T4–T5, S3–S6; moderately long on mandible, ventral surface of front coxa and trochanter, dorsal surface of tarsi and mid and hind tibiae, T4–T5 laterally; very long on posterior margin of mid and hind basitarsi. S2 with black, suberect, moderately short hairs, which are branched only apically.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and moderately finely punctate; coarser on adjacent convex area; lower  $1/3$  longitudinally striate. Malar area longitudinally striate (except substrigulate below). Supraclypeal area imbricate on disc; lateral slopes with crowded punctures. Paraocular area punctures crowded; moderately coarse below; slightly finer above; interspaces rugulose throughout. Frontal area densely and coarsely punctate; interspaces rugulose and dull. Vertexal area minutely punctate; interspaces smooth. Mesoscutum densely and moderately coarsely punctate on anterior  $1/3$ , interspaces imbricate; sparser and coarser on posterior  $2/3$ , interspaces smooth. Scutellum, metanotum and mesepisternum moderately coarsely and densely punctate (except metanotum punctures crowded); interspaces imbricate and dull. Metepisternum obliquely striate medially; rugulose above and below. Lateral surface of propodeum imbricate (except rugose on anterior  $1/4$ ) but somewhat shiny. Upper area

of vertical surface of metapostnotum rugulose medially. Metasomal terga minutely punctate; T1 sparsely punctate; T2–T5 moderately densely punctate; interspaces smooth throughout. Metasomal sterna minutely (except moderately finely on S6) and moderately densely punctate (except sparsely punctate on mid-longitudinal band); interspaces imbricate throughout.

MALE (Figs. 8B, 8D, 8F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 8.8–9.4; head width 2.9–3.2; head length 2.5–2.7; intertegular distance 2.4–2.7; forewing length 6.5–6.8.

*Colouration*: Tibial spurs, tarsi, wing veins pale-brown. Tibiae, marginal zones of T2–T5, posterior 1/5 of S2–S5 dark-brown.

*Structure*: Labrum medially flat. Clypeal mid-longitudinal area evenly shallowly and broadly (= MOD) depressed; apicomedial ridge absent. Malar area ~2.4x as long as basal depth of mandible (39:16). UID:LID (68:59). Horizontal surface of metapostnotum ~0.45x as long as metanotum (21:45). Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus 3.75x longer than broad (60:16). Outer rami of hind tarsal claws ~1.3x as long as inner rami (23:18). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 9A, 9B, 9C, respectively.

*Pubescence*: Pale-yellow on clypeus, supraclypeal and frontal areas, mid and hind tarsi. Vertexal and genal areas, mesepisternum, metepisternum, coxae, trochanters, femora with pale-yellow hairs intermingled with black ones. Lateral surface of propodeum without off-white appressed hairs. Ventral surface of hind coxa and trochanter with plumose, long hairs. S2 with moderately long setae. Marginal zones of S2–S5 with a line of off-white, plumose, erect, moderately short hairs.

*Surface sculpture*: Clypeus without irregular sulci; mid-longitudinal depression punctures crowded; adjacent convex area with very sparse punctures. Supraclypeal area smooth. Paraocular area densely punctate. Vertexal area moderately finely punctate. Clypeal anterior 1/3, scutellum and mesepisternum with smooth interspaces. Metepisternum rugose above. Lateral surface of propodeum rugulose. Metasomal terga moderately finely punctate; T1 moderately densely punctate. T2–T5 and metasomal sterna densely punctate.



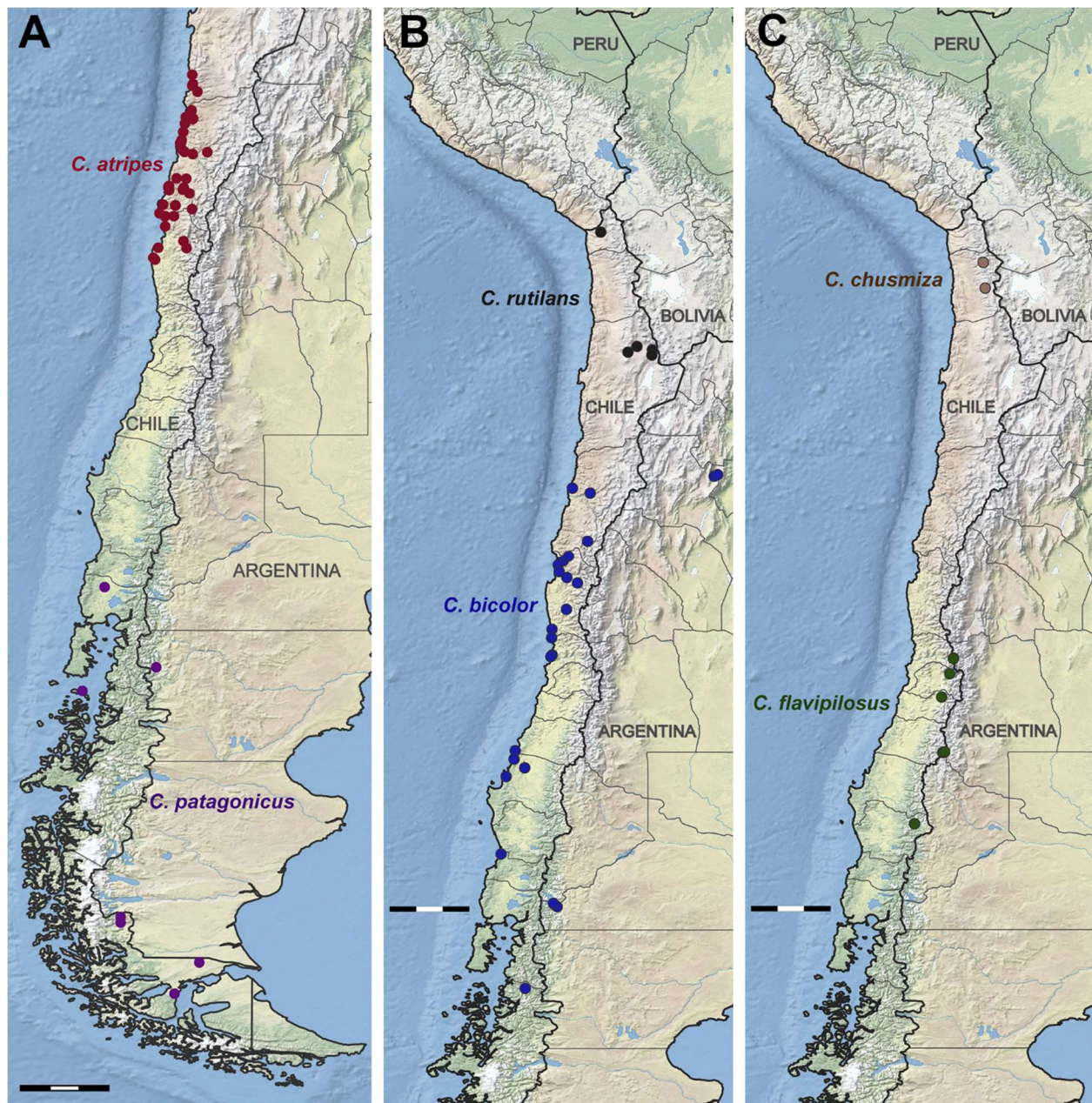
**Figure 9.** Dorsal view of the male terminalia of *C. atripes*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied: CHILE – Region II:** 5km N of Paposo, (-24.958, -70.468), 342m, 25/x/2000, [L.Packer], 1♂, {PCYU}. 6km N of Taltal, (-25.375, -70.450), 9m, 20/xi/2002, [Grixti & Zayed], 1♀, {PCYU}; idem, except 15km SE of Taltal, (-25.480, -70.391), 854m, 21/xi/2002; idem, except 16km N of Taltal, (-25.264, -70.437), 41m, 4/x/2002, 8♀♀; idem, except 16km N of Taltal, (-25.264, -70.437), 41m, 20/xi/2002, [Grixti & Zayed], 1♂. **Region III:** 1km N of Caldera, (-27.057, -70.802), 17m, 14/x/2009, [J.Gibbs], 6♀♀, {PCYU}; idem, except 16/x/2009, 1♀; idem, except 18/x/2009, 2♀♀. 8km W of Domeyko, (-28.979, -70.972), 646m, 15/x/2014, [J.Postlethwaite], 1♂, {PCYU}. 9km N of Chañaral, (-26.278, -70.659), 30m, 16/x/2010, [Almeida & Packer], 1♂, {RPSP}. 10km N of Caldera, (-26.977, -70.786), 36m, 14/x/2010, [Almeida & Packer], 1♀, {RPSP}. 10km N of Huasco Bajo, (-28.380, -71.166), 76m, 13/x/2001, [L.Packer], 1♂, {PCYU}. 10km W of Domeyko, (-28.978, -70.984), 634m, 13/x/2010, [Almeida & Packer], 2♂♂, {RPSP}. 37km W of Copiapó, (-27.350, -70.000), 1050m, 16/xi/2003, [M.Irwin], 1♀, {BBSL}. 51km N of Vallemar, (-28.113, -70.596), 533m, 6/xi/1992, [Rozen, Sharkov & Snider], 2♀♀, {AMNH}. 53km NNE of Vallenar, (-28.161, -70.643), 480m, 15/ix/2013, [Almeida & Packer], 1♀, {RPSP}; idem, except 17km N Vallenar, (-28.433, -70.720), 659m, 13/x/2010, 1♂; idem, except 19km N of Vallemar, (-28.419, -70.714), 672m, 13/x/2010, 2♂♂. Caldera, (-27.075, -70.832), 43m, 17/x/2014, [J.Postlethwaite], 1♀, {PCYU}. Caleta Chañaral de Aceituna, (-29.090, -70.467), 1664m, 5/v/2010, [Packer & Fraser], 3♂♂, {PCYU}. Caleta Pan de Azucar, 13/iv/2000, [L.Packer], 2♀♀1♂, {PCYU}. Camping Tres

Playitas, (-28.399, -71.188), 13m, 17/xi/2002, [Grixti & Zayed], 1♀, {PCYU}. Copiapó bypass km 16, (-27.410, -70.444), 505m, 19/v/2010, [L.Packer], 1♂, {PCYU}. Cuesta Portezuelo Blanco, (-26.324, -70.431), 408m, 17/x/2010, [Almeida & Packer], 1♂, {RPSP}. E of Chañaral, (-26.341, -70.449), 342m, 16/x/2010, [Packer & Almeida], 1♂, {PCYU}. Highway 5 km 848, (-27.344, -70.693), 192m, 16/x/2009, [J.Gibbs], 6♀♀6♂♂, {PCYU}; idem, except km 908, 14/x/2009, 1♀; idem, except km 915, 14/x/2009, 1♀. Los Medanos, (-26.474, -70.685), 38m, [L.Packer], 1♀1♂, {PCYU}. N of Huasco, (-28.440, -71.188), 17m, 19/x/2013, [S.Monckton], 7♀♀, {PCYU}; idem, except 1/x/2013, [Postlethwaite & Monckton], 1♀; idem, except 14/x/2013, [Postlethwaite & Monckton], 1♂. N of Vallenar, (-28.500, -70.750), 568m, 11/x/2000, [L. Packer], 2♀♀4♂♂, {PCYU}; idem, except 17/x/2000, 1♀2♂♂. NE Aguada de Tongoy, (-28.512, -71.166), 120m, 14/ix/2010, [L.Packer], 1♀1♂, {PCYU}. NW of Copiapó, (-27.277, -70.764), 226m, 23/x/2000, [L.Packer], 2♀♀, {PCYU}. Parque Nacional Llanos de Challe, (-28.150, -70.940), 237m, 6/x/2002, [L.Packer], 4♀♀, {PCYU}; idem, except 13/x/2000, 2♀♀. Pesquera Bahia Caldera, (-27.054, -70.804), 14m, 15/xi/2013, [Postlethwaite & Monckton], 1♂, {PCYU}. Quebrada los Leones, (-26.977, -70.786), 36m, 1/v/2010, [L.Packer], 1♀, {PCYU}. Quebrada Salada, (-26.730, -70.736), 27m, 22/x/2013, [S.Monckton], 2♀♀, {PCYU}; idem, except 15/xi/2013, [Postlethwaite & Monckton], 1♂. **Region IV:** 1km W of Lorenzo Peralta, (-30.581, -71.650), 396m, 7/xi/2015, [L.Packer], 1♀, {PCYU}. Chañar, (-30.286, -70.633), 1384m, 22/x/2009, [J.Gibbs], 3♀♀, {PCYU}. Choros Bajos, (-29.285, -71.316), 48m, 16/x/2000, [L.Packer], 2♀♀, {PCYU}. Los Choros, (-29.313, -71.293), 150m, 13/ix/2010, [L.Packer], 1♂, {PCYU}. N of Punta de Choros, (-29.220, -71.462), 24m, 8/xi/2013, [L.Packer], 1♀, [Postlethwaite & Monckton], 1♀, {PCYU}. Parque Nacional Fray Jorge, (-30.637, -71.597), 259m, 14/x/2000, [L.Packer], 1♀, {PCYU}. Playa la Despensa, (-29.620, -71.287), 4m, 11/xi/1997, [L.Packer], 2♀♀1♂, {PCYU}. S of Vicuña, (-30.072, -70.727), 748m, 14/x/2014, [J.Postlethwaite], 1♀, {PCYU}. SE of Los Choros, (-29.305, -71.283), 136m, 13/ix/2010, [L.Packer], 3♂♂, {PCYU}. Tongoy Arda Costanera, (-30.272, -71.498), 4m, 26/x/2001, [Packer & Fraser], 1♀, {PCYU}.

**Range:** Chile (Regions II–IV). See also Fig. 10A.





**Figure 10.** Geographic distribution by *Colletes* species. (A) *C. atripes* and *C. patagonicus*; (B) *C. rutilans* and *C. bicolor*; (C) *C. chusmiza* and *C. flavipilosus* **n. sp.** The records of *C. rutilans* out of Chile have not been plotted. Scale bars approximately 300 km.

**Biogeographic distribution:** South American transition zone: Atacama province. Andean region: Chilean sub-region (Coquimban province). Central Chilean species distributed in the winter rainfall area at altitudes of 0–1700m a.s.l.



**DNA barcode:** Available. BOLD: ACF589 (5♀♀2♂♂), BOLD: AAF4094 (6♂♂).

Representatives of both BINs are distributed throughout the species' geographical range (see Table S1). Distance between BINs: 1.65–2.79%. Distance from the nearest neighbour (*C. cognatus*): 5.56–8.18%.

**Floral hosts:** Leguminosae – *Adesmia confusa* Ulibarri [Jaffuel & Pirion 1926 (as *A. arborea* Clos)]. Loasaceae – *Nasa triphylla* (Juss.) Weigend (this study). Malvaceae – *Cristaria* sp. (Toro 1999). Portulacaceae – *Calandrinia* sp. (Toro 1999). Solanaceae – *Nolana* sp. (this study).

**Comments:** Although *C. atripes* has a reasonably restricted geographic range within Chile (Regions II–IV), the species is very common where it is found.

Determination of the actual identity of *C. atripes* was straightforward, as the female is unique in having the combination of mesosomal dorsum and T1 covered with ferruginous pubescence and black metasoma, as indicated in the original description by Spinola (as *C. dimidiata*). DNA barcoding allowed for easy sexual association.

Even though two different BINs have been assigned to specimens identified as *C. atripes*, which could suggest the existence of an additional cryptic undescribed species, no consistent morphological support has been found (including comparison between the terminalia of potentially distinct males from each BIN). Therefore, a scenario of high level of intraspecific variation in COI seems to be more likely than two sibling species evolving sympatrically (see Table S1).

### ***Colletes bicolor* Smith, 1879**

(Figs. 11A–F)

*Colletes bicolor* Smith, 1879: 3; Dalla Torre 1896: 38; Cockerell 1904: 276, 1909: 398, 1919: 208; Friese 1906: 89, 1910: 642; 1912: 366; Schrottky 1907: 5, 1913: 236; Jensen-Haarup 1908: 99; Jörgensen 1909: 221, 1912a: 300, 1912b: 92; Claude-Joseph 1926: 131; Jaffuel & Pirion 1926: 364; Gazulla & Ruiz 1928: 300; Ruiz 1936: 165, 1944: 206; Toro 1986: 122, 1999: 27; Rojas & Toro 1993: 86; Moure & Urban 2002: 5; Moure *et al.* 2007: 679; Almeida & Danforth

2009: 293; Kuhlmann *et al.* 2009: 296; Montalva & Ruz 2010: 21; Almeida *et al.* 2011: 7; Ascher & Pickering 2017.

Lectotype ♀ (examined). {NHM}. [hereby designated]

*Biglossa andina* Jörgensen, 1909: 221. Synonymy proposed by Jörgensen (1912a: 300).

Syntypes ♀ and ♂ (not examined). {whereabouts unknown}.

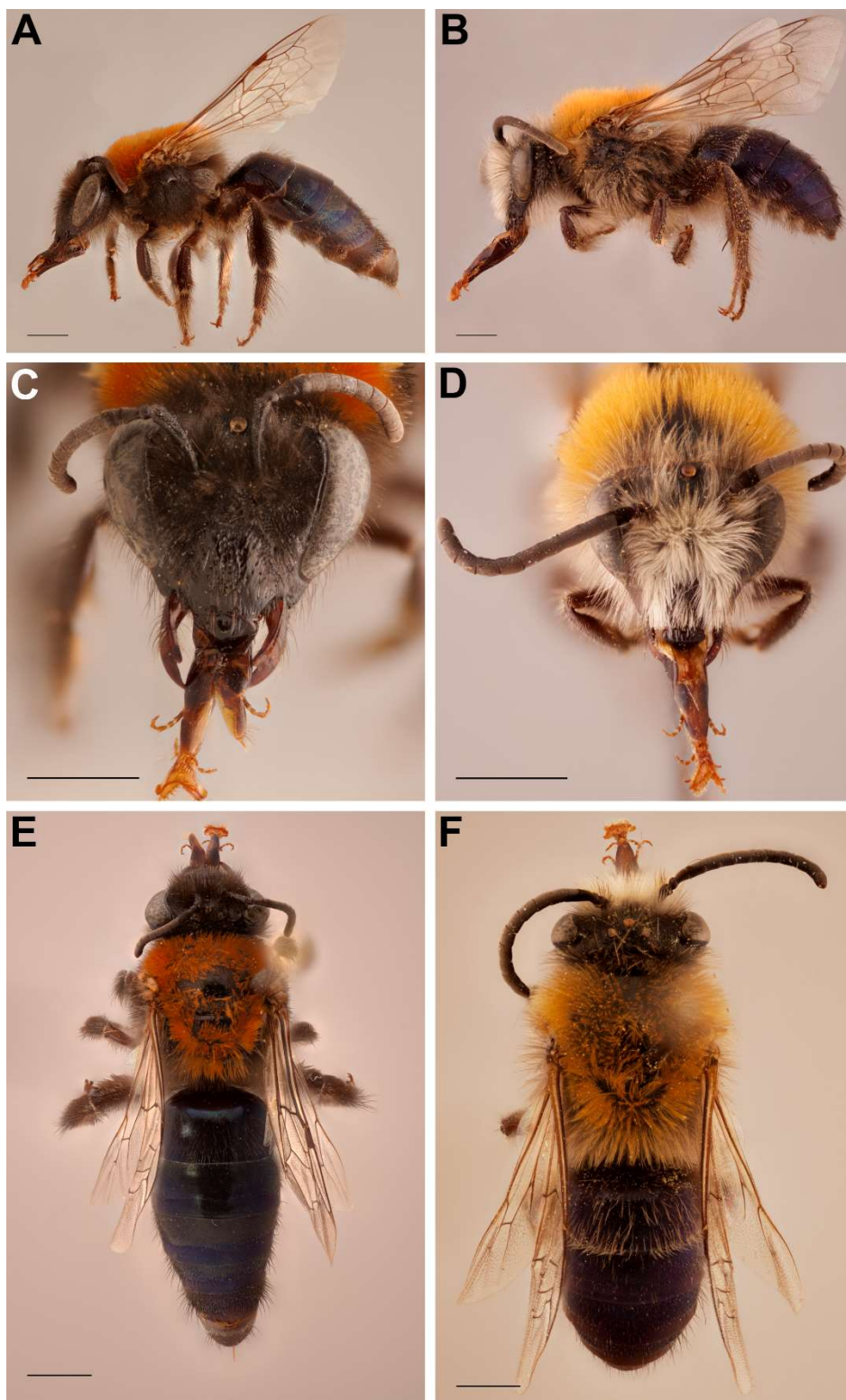
**Diagnosis:** The combination of pubescence on mesosomal dorsum ferruginous, and metasoma metallic blue is sufficient to distinguish *C. bicolor* from all Chilean species of the genus, except *C. flaminii* and *C. fulvipes*. From the former, *C. bicolor* can be differentiated by the mesepisternal interspaces smooth (interspaces imbricate in *C. flaminii*); female malar area 0.7x as long as basal depth of mandible (malar area 1.4x as long as basal depth of mandible in *C. flaminii*); and male paraocular area with black hairs (paraocular area without black hairs in *C. flaminii*). *Colletes bicolor* can be readily differentiated from *C. fulvipes* by the black tibiae (tibiae pale-orange in *C. fulvipes*).

**Redescription:** FEMALE (Figs. 11A, 11C, 11E):

*Dimensions (mm):* Approximate body length 10.5–11.6; head width 3.2–3.6; head length 2.5–2.8; intertegular distance 2.5–2.9; forewing length 7.3–8.0.

*Colouration:* Black except metallic blue on metasomal terga (except T6 black). Metallic dark-blue on metasomal sterna (except S6 dark-brown). Reddish-brown on distal half of tarsal claws; marked on distal half of mandible. Pale-orange on tegula, proximal half of tarsal claws. Dark-brown on tibial spurs, distitarsi, stigma, wing veins (except veins C, R and M+Cu of forewing black).

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area neither depressed nor carinate; adjacent lateral area convex; apicomedial ridge absent. Malar area ~0.7x as long as basal depth of mandible (30:44). F1 ~1.1x as long as its apical width (38:34). UID:LID (72:63). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum half as long as metanotum (20:40); metapostnotal pits well-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa bearing short spine (0.5x MOD). Posterior hind tibial spur ciliate. Hind basitarsus ~3.6x longer than broad (55:15).



**Figure 11.** *Colletes bicolor* Smith, 1879. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

Outer rami of hind tarsal claws 2x as long as inner rami (40:20). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Black, plumose, erect, long on lateral slopes of clypeus and supraclypeal area, interantennal, paraocular, frontal and genal areas, mesepisternum, metepisternum, ventral surface of front coxa, posteroventral surface of front femur, ventral surface of mid trochanter, ventral margin of mid femur, T1 (except suberect, moderately long laterally), S1; such hairs very long on vertexal area, upper margin of lateral surface of propodeum, ventral surface of hind coxa and trochanter. Pronotal lobe with mixed off-white and black, plumose, erect, moderately long hairs. Ferruginous, plumose, erect, moderately long on mesoscutum, scutellum; such hairs long on metanotum. Black, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. Fulvous, suberect, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Black, erect, short setae on discs of T2–T3; moderately short on dorsal surface of front and mid tibiae and mid basitarsus, T2–T3 laterally, S3–S6; moderately long on mandible, posterior surface of front tibia, dorsal surface of front tarsus, T4–T5 laterally. S2 with black, erect, moderately short hairs, which are branched only apically.

*Surface sculpture:* Mid-longitudinal depressed area densely and moderately finely punctate; sparser and coarser on adjacent convex area; lower 1/3 longitudinally striate. Malar area with very sparse punctures; interspaces substrigulate. Supraclypeal area imbricate on disc; lateral slopes punctures crowded. Paraocular area punctures crowded and moderately coarse (except coarsely punctate towards antennal socket); interspaces shiny. Frontal area punctures crowded and coarse. Vertexal area with very sparse moderately fine punctures; interspaces smooth and shiny. Mesoscutum and scutellum densely and moderately coarsely punctate (except mesoscutal disc sparsely punctate and scutellar posterior 1/3 with crowded punctures); interspaces smooth and shiny throughout. Metanotum punctures crowded. Mesepisternum densely and coarsely punctate; interspaces smooth above, rugulose below. Metepisternum obliquely striate medially; rugose above and below. Punctuation on lateral surface of propodeum difficult to discern from the overall rugulose integument. Upper area of vertical surface of metapostnotum rugose medially. Metasomal terga minutely punctate; interspaces smooth and shiny. Metasomal sterna finely and moderately densely punctate (except sparsely punctate on mid-longitudinal band); interspaces imbricate.

MALE (Figs. 11B, 11D, 11F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 8.9–9.8; head width 3.2–3.5; head length 2.5–2.7; intertegular distance 2.5–2.8; forewing length 7.4–7.8.

*Colouration*: Wing veins pale-brown (except veins C, R, and M+Cu of forewing dark-brown). Basitarsi dark-brown (except distitarsi pale-brown). T6 metallic blue.

*Structure*: Clypeal mid-longitudinal area narrowly (0.5x MOD) depressed on upper half; depression progressively broadening towards lower margin. Malar area ~1.4x as long as basal depth of mandible (34:24). F1 ~0.9x as long as its apical width (34:38). UID:LID (70:57). Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum half as long as metanotum (22:40). Posteromedial surface of front coxa without spine. Hind basitarsus ~3.6x longer than broad (47:13). Outer rami of hind tarsal claws ~1.4x as long as inner rami (32:22). S7, S8 and genital capsule as in Figs. 12A, 12B, 12C, respectively.

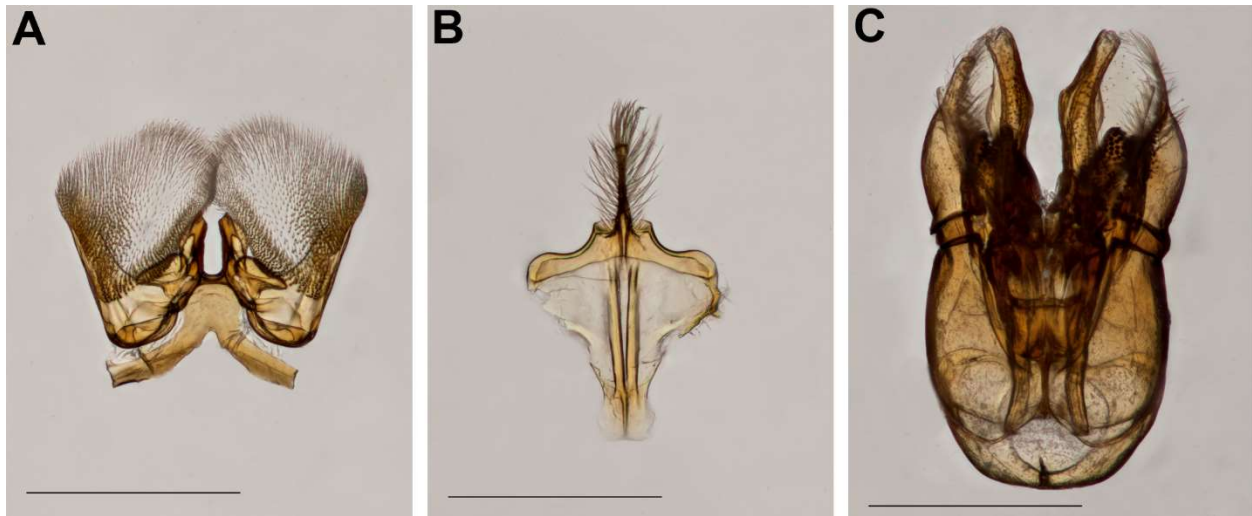
*Pubescence*: Pale-yellow on lateral slopes of clypeus and supraclypeal area, interantennal and paraocular areas (except for longitudinal band of black hairs near inner margin of compound eye). Frontal, vertexal and genal areas, mesepisternum, legs with fuscous hairs intermingled with pale-yellow ones. Pronotal lobe without black hairs. Moderately long on metasomal sterna. S2 with plumose hairs. Marginal zones of S2–S5 with transverse line (complete on S2, interrupted medially on S3–S5) of off-white, plumose, erect, moderately short hairs.

*Surface sculpture*: Clypeal mid-longitudinal depressed area densely punctate. Supraclypeal area rugulose. Paraocular area densely and moderately finely punctate. Vertexal interspaces rugulose. Mesoscutal anterior 1/3 moderately densely punctate. Mesepisternum moderately coarsely punctate. Lateral surface of propodeum with smooth interspaces. Metasomal terga finely punctate; moderately dense on T1–T2; sparse elsewhere.

**Material studied:** *Primary type specimen*: Lectotype ♀ of *C. bicolor* – “Type”. “B.M. TYPE; HYM.; 17.a.534”. “Colletes; bicolor.; Sm.; (Type)”. “Mendoza”. “SYN-; TYPE”. “♀ SYNTYPE; Colletes; bicolor Smith 1879: 3; det. D. Notton 2016”. “LECTOTYPE; Colletes bicolor ♀; Smith, 1879; designated R. Ferrari, 2017”. {NHM}. [hereby designated].

*Secondary type specimen*: Paralectotype ♀ of *C. bicolor* – **ARGENTINA – Mendoza**: 1♀, {NHM}.





**Figure 12.** Dorsal view of the male terminalia of *C. bicolor*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Additional specimens:* **ARGENTINA – Catamarca:** 5km NE of Santa Maria, (-26.651, -66.013), 1886m, 18/ii/2003, [L.Packer], 1♀, {PCYU}. **Tucumán:** 25km ESE of Amaicha del Valle, (-26.600, -65.895), 2065m, 25/x/2004, [E.Almeida], 1♀, {UFMG}. **CHILE – Region III:** 1km N of Caldera, (-27.057, -70.802), 17m, 16/x/2009, [J.Gibbs], 1♀1♂, {PCYU}. Caldera, (-27.057, -70.805), 15m, 17/x/2014, [J.Postlethwaite], 1♂, {PCYU}. Canto del Agua, (-27.380, -70.344), 443m, 21/x/1969, [Rozen & Peña], 1♀, {AMNH}. Chancoquin, (-28.848, -70.285), 1210m, 27/x/1980, [L.Peña], 1♀, {AMNH}. Las Juntas, 5/x/1982, [Montenegro], 1♀, {AMNH}. Pesquera Bahia Caldera, (-27.054, -70.804), 14m, 15/xi/2013, [Postlethwaite & Monckton], 1♀, {PCYU}. **Region IV:** 7km N of Los Vilos, (-31.849, -71.493), 76m, 11/x/2003, [M.Irwin], 1♀♂, {BBSL}; idem, except 25/xii/2003, [Parker & Irwin], 2♀♀. 10km SW of Combarbala, (-31.235, -71.088), 910m, 31/x/1994, [Leschen & Carlton], 1♂, {KUNHM}. 15km S of La Villa, (-30.104, -70.990), 470m, 21/xi/2003, [Irwin & Parker], 1♀2♂♂, {BBSL}. Chañar, (-30.286, -70.633), 1384m, 22/x/2009, [J.Gibbs], 1♀, {PCYU}. Islón, (-29.892, -71.179), 106m, 28/xi/1955, [Wagenknecht], 1♀, {KUNHM}. Juan Soldado, (-29.917, -71.254), 22m, 13/xii/1956, [Wagenknecht], 2♀♀, {KUNHM}. La Serena, (-29.896, -71.253), 15m, 19/xi/1955, [Wagenknecht], 3♂♂, {KUNHM}. Pichidangui, (-32.138, -71.506), 17m, 10/ii/2003, [F.Parker], 1♂, {BBSL}. Tres Cruces, (-29.370, -70.933), 526m, i/1997, [U.Peña], 1♂, {AMNH}. **Region V:** Horcón, 10/xi/1967, [J.Aguila], 1♂, {AMNH}. Quintero, (-32.799, -71.538), 84m, 10/i/1967,

[D.Hoz], 1♂, {AMNH}. **Region Metropolitana:** El Portezuelo, (-33.463, -70.770), 461m, xi/1978, [L.Peña], 1♀1♂, {AMNH}. **Region VII:** Tregualetu, (-35.946, -72.739), 55m, 28/xii/2006, [L.Packer], 2♀♀, {PCYU}; idem, except 17/xii/2006, 1♀2♂♂; idem, except N of Tregualetu, (-35.949, -72.735), 118m, 2/i/2013, 1♀. **Region VIII:** Cobquecura, (-36.138, -72.794), 43m, 6/ii/1983, [F.Rodriguez], 1♂, {AMNH}. Concepción, (-36.831, -73.027), 116m, 2/xii/1904, [P.Herbst], 1♂, {AMNH}. **Region X:** Llanquihue, (-41.266, -73.018), 110m, 21/ii/2003, [F.Parker], 1♀1♂, {BBSL}.

**Range:** Argentina (Catamarca, Tucumán, Mendoza), Chile (Regions III–X). See also Fig. 10B.

**Biogeographic distribution:** South American transition zone: Prepuna and Monte provinces. Andean region: Central Chilean sub-region (Coquimban and Santiagan provinces); Subantarctic sub-region (Maule and Valdivian Forest provinces). Central Chilean and Western Argentinean species distributed at altitudes of 0–2100m a.s.l.

**DNA barcode:** Available. BOLD: AAF4093 (1♀), BOLD: AAJ6724 (1♀1♂). Specimens from Chile and Argentina were assigned different BINs (see Table S1). Distance between BINs: 0.54–3.41%. Distance from the nearest neighbour (*C. nigrifolius*): 9.6–10.24%.

**Floral hosts:** Alstroemeriaceae – *Alstroemeria* sp. (Claude-Joseph 1926, Ruiz 1944). Apiaceae – *Eryngium paniculatum* Cav. & Dombey ex F. Delaroché (Claude-Joseph 1926, Ruiz 1944). Compositae – *Baccharis pingraea* DC. [Jørgensen 1909, 1912a (as *B. serrulata* (Lam.) Pers.)]; *B. salicina* Torr. & A. Gray [Jørgensen 1912a (as *B. salicifolia* (Ruiz & Pav.) Pers.)]; *Senecio* sp. (Claude-Joseph 1926, Ruiz 1944). *Senecalia gilliesii* (Steud.) Seigler & Ebinger [Jørgensen 1912a (as *Acacia furcata* Desv.)]; *Glycyrrhiza astragalina* Hook. & Arn. (Jørgensen 1912a, 1912b, Jaffuel & Pirion 1926); *Medicago sativa* L. (Jørgensen 1912a); *Prosopis alpataco* Phil. (Jørgensen 1912a, 1912b, Jaffuel & Pirion 1926); *P. campestris* Griseb. (Jørgensen 1912a). Malvaceae – *Sphaeralcea bonariensis* (Cav.) Griseb. (Jørgensen 1912a). Myrtaceae – *Myrceugenia exsucca* (DC.) O. Berg [Claude-Joseph 1926 (as *Eugenia corralensis* (Phil.))]. Ranunculaceae – *Clematis campestris* A. St. -Hil. [Jaffuel & Pirion 1926 (as *C. hilarii* Spreng.)]. Solanaceae – *Lycium chilense* Bertero [Jørgensen 1909, 1912a, 1912b, Jaffuel & Pirion 1926]; *L.*

*ciliatum* Schltdl. [Jørgensen 1912a, 1912b, Jaffuel & Pirion 1926 (as *L. argentinum* Hieron.)]; *Physalis viscosa* L. (Jørgensen 1912a); *Solanum atriplicifolium* Gill. ex Nees (Jørgensen 1912a); *S. elaeagnifolium* Cav. (Jørgensen 1912a). Tamaricaceae – *Tamarix africana* Poir. (Jørgensen 1912a).

**Comments:** *Colletes bicolor* visits, at least, 16 genera from nine plant families, which may explain the reason why this species is so common and widely distributed in central Chile and western Argentina.

***Colletes chusmiza* Rojas & Toro, 1993**

(Figs. 13A–F)

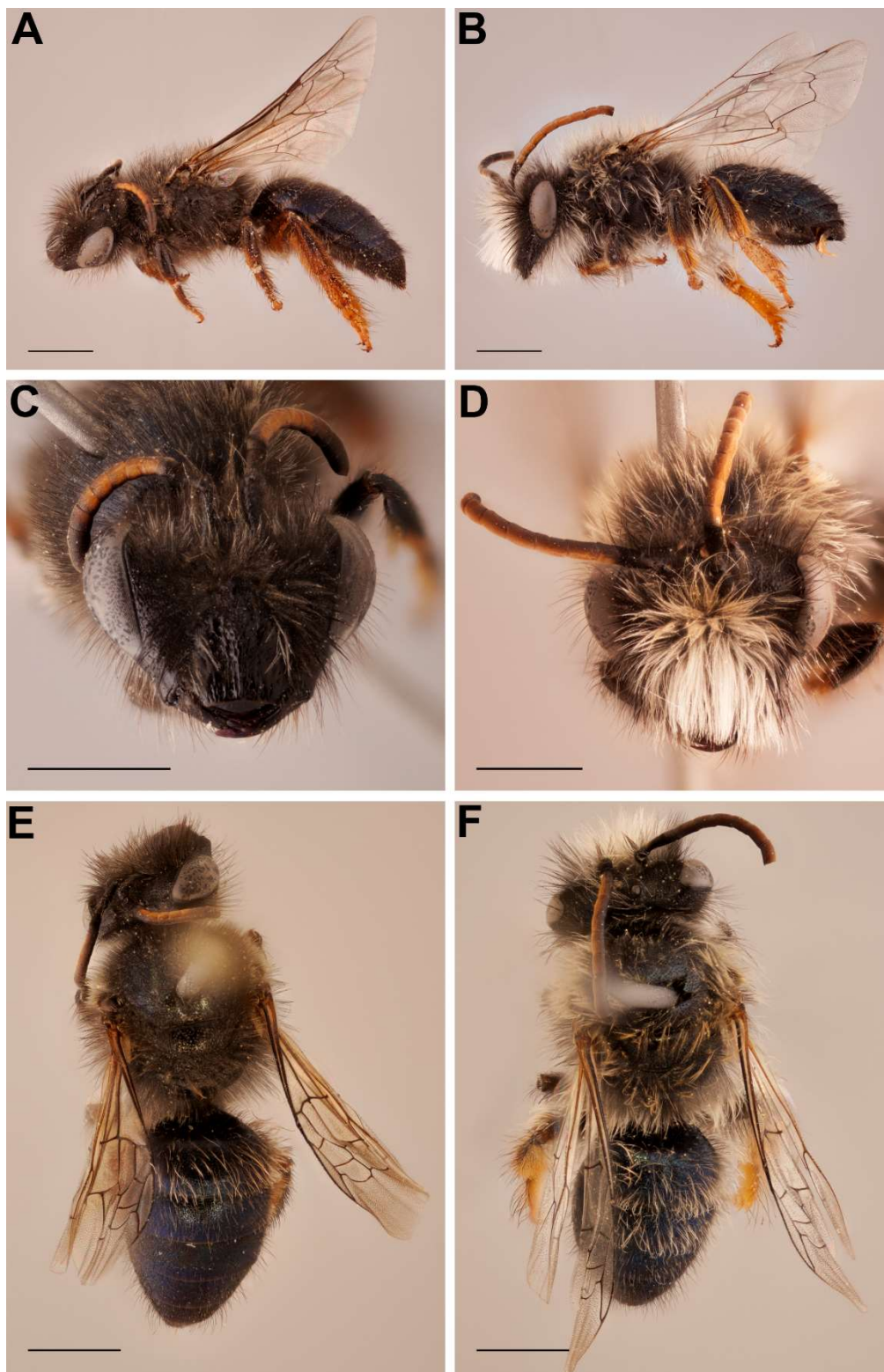
*Colletes chusmiza* Rojas & Toro, 1993: 83; Toro 1999: 27; Moure *et al.* 2007: 680; Montalva & Ruz 2010: 21; Ascher & Pickering 2017.

Holotype ♂ (examined). {AMNH}.

**Diagnosis:** The combination of clypeal mid-longitudinal area carinate, mesosomal pubescence black, and metasoma metallic blue is sufficient to differentiate *C. chusmiza* from all Chilean species of *Colletes*, except *C. vicugnensis*. However, their females (the male *C. vicugnensis* is unknown) can be differentiated by the facial pubescence with off-white and black hairs intermixed in *C. chusmiza* (facial pubescence entirely black in *C. vicugnensis*); ventral surface of F2–F8, mid and hind tibiae pale-orange in *C. chusmiza* (ventral surface of F2–F8, mid and hind tibiae black in *C. vicugnensis*); and comparatively shorter hind basitarsus, ~2.5x longer than broad, in *C. chusmiza* (hind basitarsus ~3x longer than broad in *C. vicugnensis*).

**Redescription:** FEMALE (Figs. 13A, 13C, 13E):

*Dimensions (mm):* Approximate body length 9.1–9.5; head width 3.4–3.5; head length 2.5–2.6; intertegular distance 2.5–2.7; forewing length 6.9–7.1.



**Figure 13.** *Colletes chusmiza* Rojas & Toro, 1993. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

*Colouration:* Black except metallic dark-blue on metasomal terga (except pale-brown on marginal zones). Metallic dark-green on mesoscutum. Pale-orange on distal ring of front and mid femora, distal 1/4 of dorsal surface of front tibia, tarsi, mid tibia (except proximal 2/3 of dorsal surface and proximal half of posterior surface black), tibial spurs, ventral surface and distal 2/3 of dorsal surface of posterior femur, hind tibia (except posterior surface black), distal half of tarsal claws. Dark-orange on ventral surface of F2–F8. Dark-brown on tegula, wing veins, stigma, metasomal sterna (except marginal zones of S1–S5 pale-brown). Reddish-brown marked on distal 1/3 of mandible. Pale-yellow on proximal half of tarsal claws.

*Structure:* Labrum medially flat and without ridges. Clypeal mid-longitudinal area with a strong, complete carina (except absent for upper 1/5); adjacent area declivous. Malar area ~1.5x as long as basal depth of mandible (31:21). F1 ~1.7x as long as its apical width (49:29). UID:LID (75:73). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum about half as long as metanotum (22:41); metapostnotal pits well-delimited; posterior transverse carina sinuous and broadly interrupted medially. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~2.5x longer than broad (58:23). Outer rami of hind tarsal claws 2.75x as long as inner rami (22:8). Posterolateral area of S6 flat and lacking carina; marginal zone not depressed.

*Pubescence:* Black, plumose, erect, long on lateral slopes of clypeus and supraclypeal area, interantennal and paraocular areas, scutellum, metanotum, mesepisternum, central area of lateral surface of propodeum, posteroventral surface of front femur, anteroventral surface of mid and hind trochanters, ventral margin of mid femur; such hairs moderately long on metepisternum, ventral surface of mid and hind coxae; very long on upper margin of lateral surface of propodeum. Frontal, genal and vertexal areas and mesoscutum with mixed off-white and black, plumose, erect, long hairs; such hairs moderately short on pronotal lobe. Black, erect, moderately short setae on ventral surface of front trochanter, disc of T3, S3–S6; such hairs moderately long on mandible (except fulvous), posterior surface of front tibia and basitarsus, dorsal surface of mid and hind tibiae and basitarsi, T4 laterally, disc of T5; long on T5 laterally; very long on posterior margin of mid and hind basitarsi. Pale-orange, suberect, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Pale-orange, suberect, very



long hairs, which are branched only apically on anterior surface of hind femur and tibia. S1–S2 with mixed moderately short hairs, which are branched only apically, and long, plumose hairs.

*Surface sculpture:* Clypeus longitudinally striate adjacently to mid-longitudinal carina and lower margin; flat area with very sparse moderately coarse punctures. Malar area densely and moderately coarsely punctate on upper 3/4; substrigulate on lower 1/4. Supraclypeal area imbricate but somewhat shiny. Paraocular area punctures crowded and moderately fine; interspaces shiny. Frontal area densely and moderately coarsely punctate; interspaces imbricate and dull. Vertexal area finely and moderately coarsely punctate (denser close adjacently to lateral ocellus); interspaces smooth and shiny. Mesoscutum, scutellum, metanotum densely and moderately coarsely punctate (except sparsely punctate on mesoscutal mid-posterior area); interspaces smooth on mesoscutum, imbricate on scutellum, rugulose on metanotum. Mesepisternum moderately densely and moderately coarsely punctate; interspaces imbricate. Metepisternum rugulose above; obliquely striate medially; imbricate below. Lateral surface of propodeum imbricate. Upper area of vertical surface of metapostnotum smooth medially. T1 finely and moderately densely punctate; interspaces imbricate. T2–T5 finely and densely punctate; interspaces rugulose on discs, imbricate on marginal zones. Metasomal sterna finely and moderately densely punctate; interspaces imbricate.

MALE (Figs. 13B, 13D, 13F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.9–9.2; head width 3.2–3.4; head length 2.3–2.4; intertegular distance 2.3–2.5; forewing length 6.7–7.1.

*Colouration:* Proximal half of ventral surface of F9 dark-orange. Mesoscutum black. Hind femur mostly black (except distal ring pale-orange).

*Structure:* Clypeal mid-longitudinal area with a weak carina on lower half. Malar area ~1.8x as long as basal depth of mandible (58:32). F1 1.25x as long as its apical width (40:32). UID:LID (74:65). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded. Horizontal surface of metapostnotum 0.45x as long as metanotum (18:40); posterior transverse carina sinuous and narrowly interrupted medially. Hind basitarsus ~2.1x longer than broad (58:27). Outer rami of hind tarsal claws 2.25x as long as inner rami (18:8). S7, S8 and genital capsule as in Figs. 14A, 14B, 14C, respectively.

*Pubescence:* Off-white on lateral slopes of clypeus and supraclypeal area, interantennal area. Off-white and black hairs intermixed on scutellum, metanotum, mesepisternum, metepisternum, legs, T1, S1. Setae on dorsal surface of mid and hind tibiae and tarsi pale-yellow. S1–S2 with plumose hairs only. S3–S6 with minute setae.

*Surface sculpture:* Supraclypeal and frontal areas punctures crowded. Vertexal area densely punctate. Mesoscutal anterior 1/3 sparsely punctate. Metepisternum rugulose below. T1 densely and moderately finely punctate; interspaces rugulose. S2 and mid-longitudinal area of S3–S5 sparsely punctate.

**Material studied:** *Primary type specimen:* Holotype ♂ – “HOLO; TIPO”. “I Region; Chusmiza; 15-x-1981”. “Colletes; chusmiza n.sp; 1993”. “AMNH\_IJC 00324328”. {AMNH}.

*Secondary type specimens:* Paratypes ♀♀ and ♂♂ – **CHILE – Region I:** Chusmiza, (-19.682, -69.188), 3419m, 15/x/1981, [V.Cabezas], 1♀, {PUCV}; idem, except [J.Vial], 1♀1♂; idem, except [F.Rodriguez], 1♂; idem, except [H.Toro], 1♀, {AMNH}; idem, except [V.Cabezas], 1♂, {AMNH}; idem, except [O.Martinez], 1♂, {AMNH}; idem, except [E.Tosti-Croce], 1♂, {AMNH}; idem, except [O.Martinez], 1♀, {KUNHM}.

*Additional specimens:* **CHILE – Region I:** Highway 687 km 83, (-20.299, -69.057), 4/xi/2013, [S.Monckton], 1♀1♂, {PCYU}.

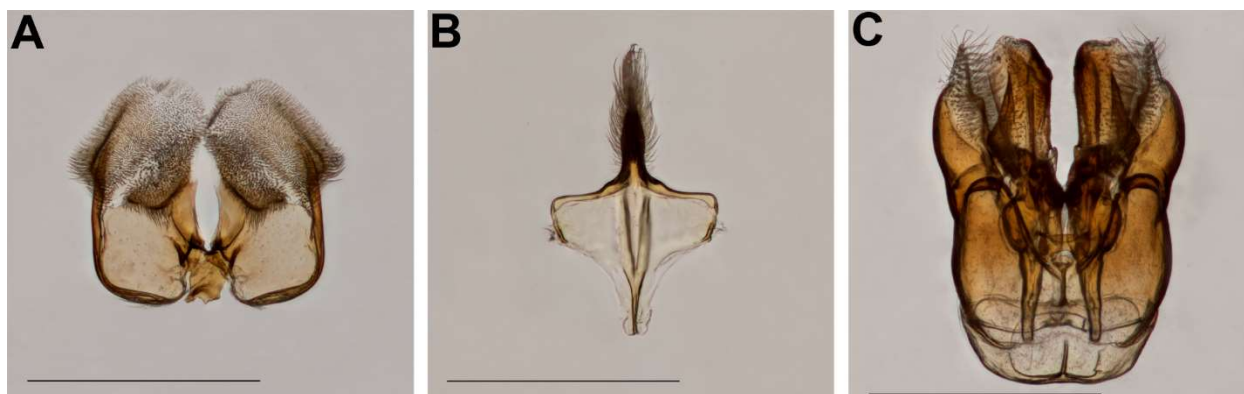
**Range:** Chile (Region I). See also Fig. 10C.

**Biogeographic distribution:** South American transition zone: Atacama province. Northern Chilean species distributed in the summer rainfall area at altitudes above 3,000m a.s.l.

**DNA barcode:** Available. BOLD: ACW1705 (1♀1♂). Distance from the nearest neighbours: 3.53–3.69% (*C. fulvipes*) and 6.1–6.12% (*C. flaminii*).

**Floral hosts:** Leguminosae – *Adesmia* sp. (Toro 1999).

**Comments:** Rare species that seems to be found only at very high altitudes in Region I.



**Figure 14.** Dorsal view of the male terminalia of *C. chusmiza*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

### ***Colletes cognatus* Spinola, 1851**

(Figs. 15A–F)

*Colletes cognata* Spinola, 1851: 223; Vachal 1909: 54.

Lectotype ♂ (not examined) designated by Moure & Urban (2002: 7). {MRSN}.

*Colletes cognatus*; Dalla Torre 1896: 38; Friese 1910: 642, 1912: 366; Ruiz 1944: 209; Toro 1986: 122, 1999: 27; Moure & Urban 2002: 7; Moure *et al.* 2007: 680; Montalva & Ruz 2010: 21; Ascher & Pickering 2017.

**Diagnosis:** The combination of mesoscutal pubescence pale-yellow, mesepisternal punctation comprised of coarse punctures intermingled with minute ones, and marginal zones of T1–T5 covered with appressed hairs is sufficient to distinguish *C. cognatus* from all *Colletes* species found in Chile.

*Colletes cognatus* is most similar to *C. arthuri* **n. sp.**, but the females can be differentiated from each other by the absence of appressed hairs on discs of T2–T5 in *C. cognatus* (discs of T2–T5 covered with pale-yellow, dense appressed hairs in the female *C. arthuri* **n. sp.**). The male of these species can be distinguished by the comparatively short malar area, ~1.5x as long as basal depth of mandible, in *C. cognatus* (malar area ~2x as long as basal depth of mandible in *C. arthuri* **n. sp.**); and mesepisternum with coarse and minute punctures intermingled in *C. cognatus* (mesepisternum with only moderately coarse punctures in *C. arthuri* **n. sp.**).

**Redescription:** FEMALE (Figs. 15A, 15C, 15E):

*Dimensions (mm):* Approximate body length 9.1–9.7; head width 3.1–3.4; head length 2.4–2.5; intertegular distance 2.3–2.5; forewing length 6.6–7.0.

*Colouration:* Black except reddish-brown on distal half of tarsal claws; marked on distal 1/3 of mandible. Pale-brown on tegula, wing veins (except vein R of forewing dark-brown), ventrally reflexed lateral areas of T1–T2. Dark-brown on tarsi, marginal zones of T1–T5, disc of S6. Pale-yellow on tibial spurs, marginal zones of metasomal sterna. Bright-yellow on proximal half of tarsal claws.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area neither depressed nor carinate; adjacent lateral area convex; apicomedial ridge absent. Malar area subequal to basal depth of mandible (35:37). F1 ~1.2x as long as its apical width (34:28). UID:LID (65:58). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded. Horizontal surface of metapostnotum ~0.4x as long as metanotum (18:46); metapostnotal pits well-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa bearing very long spine (0.7x MOD). Posterior hind tibial spur pectinate. Hind basitarsus 3.2x longer than broad (48:15). Outer rami of hind tarsal claws ~2x as long as inner rami (30:16). Posterolateral area of S6 convex and lacking carina; marginal zone depressed.

*Pubescence:* Off-white, plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, paraocular, interantennal, frontal and genal areas (except suberect and moderately short above), posteroventral surface of front trochanter and femur, mid coxa and trochanter (except short on dorsal surface), ventral margin of mid femur, T1, S1; such hairs long on mesepisternum, metepisternum, upper margin of lateral surface of propodeum. Pale-yellow, plumose, erect, moderately long on pronotal lobe, mesoscutum, scutellum, metanotum. Off-white, erect, moderately short hairs, which are branched only apically on hind coxa and trochanter; such hairs suberect, very long on anterior surface of hind femur and tibia. Pale-yellow, suberect, moderately long setae on dorsal surface of tibiae and basitarsi; erect on mandible, front coxa; very long on posterior margin of mid and hind basitarsi. Bright-yellow, suberect, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Off-white, dense appressed hairs on marginal zones of T1–T5; slightly sparser on lateral surface of propodeum.



**Figure 15.** *Colletes cognatus* Spinola, 1851. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.



Discs of T2–T5 with pale-yellow, suberect, minute setae (mixed with fulvous, erect, moderately short setae on T4–T5); such hairs long on discs of S3–S6. S2 with off-white, erect, moderately short hairs, which are branched only apically.

*Surface sculpture:* Clypeal mid-longitudinal area and lower 1/4 longitudinally striate; convex area sparsely punctate. Malar area densely and moderately coarsely punctate on upper half (interspaces rugulose); substrigulate below. Supraclypeal area impunctate and smooth (except imbricate on lower 1/4). Lower paraocular area punctures crowded; interspaces rugulose. Upper paraocular area densely and moderately finely punctate; interspaces smooth and shiny. Frontal area punctures crowded; interspaces rugose and dull. Vertexal area minutely punctate anteriorly; coarser towards occipital area; interspaces smooth anteriorly, rugulose posteriorly. Mesoscutum and scutellum densely and moderately coarsely punctate (except mesoscutal mid-posterior area sparsely punctate on and scutellar posterior 1/4 punctures crowded); interspaces smooth and shiny throughout. Metanotum punctures crowded; interspaces rugulose. Mesepisternum punctures crowded above; densely punctate below; punctation comprised of coarse punctures intermingled with minute ones anteriorly. Metepisternum obliquely striate medially; rugose above; rugulose below. Lateral surface of propodeum finely punctate; interspaces smooth (except rugose posteriorly). Upper area of vertical surface of metapostnotum transversely striate medially. Metasomal terga minutely punctate; sparsely punctate on T1; denser elsewhere; interspaces smooth (except imbricate on T5). Metasomal sterna shallowly and moderately finely punctate; moderately densely punctate on S2; denser on S3–S4 and S6; densest on S5.

MALE (Figs. 15B, 15D, 15F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.6–9.1; head width 3.0–3.2; head length 2.4–2.5; intertegular distance 2.2–2.4; forewing length 6.6–6.9.

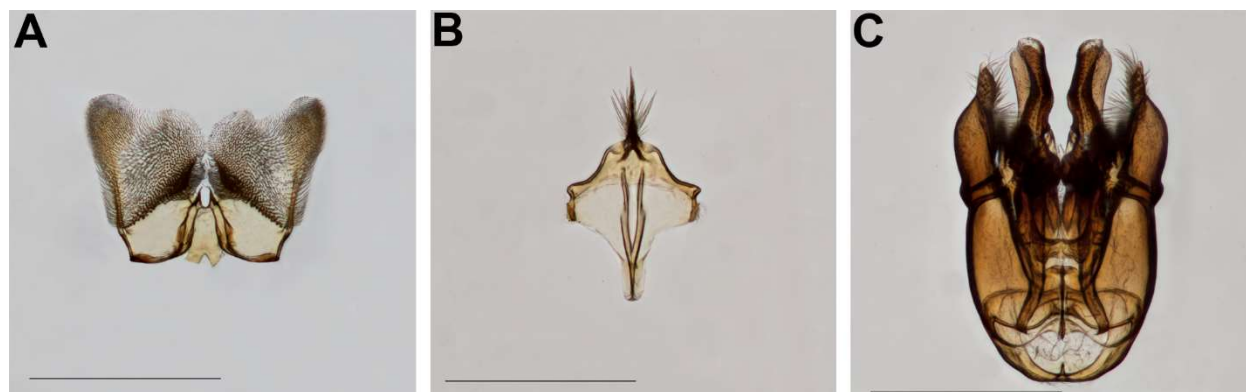
*Colouration:* Tarsal claws pale-brown. Posterior 1/3 of S1–S5 dark-brown.

*Structure:* Labrum medially convex; convexity not margined by ridges. Clypeal mid-longitudinal area evenly narrowly (0.45x MOD) and shallowly depressed on upper 3/4. Malar area ~1.5x as long as basal depth of mandible (34:22). F1 nearly as long as its apical width (30:32). UID:LID (69:56). Genal area concave behind upper summit of compound eyes in lateral

view. Horizontal surface of metapostnotum 0.45x as long as metanotum (22:49). Posteromedial surface of front coxa without spine. Hind basitarsus 3.4x longer than broad (44:13). Outer rami of hind tarsal claws 1.7x as long as inner rami (22:13). Posterolateral area of S6 flat; marginal zone not depressed. S7, S8 and genital capsule as in Figs. 16A, 16B, 16C, respectively.

*Pubescence*: Lateral surface of propodeum with erect, long hairs; without appressed hairs. T1 with long pubescence. Marginal zones of S2–S5 with a line of plumose, erect, moderately short hairs.

*Surface sculpture*: Clypeal mid-longitudinal with well-delimited fine punctures; adjacent convex area impunctate; interspaces smooth throughout. Supraclypeal area with moderately coarse punctures. Vertexal interspaces smooth throughout. Lateral surface of propodeum with rugulose interspaces anteriorly. Metasomal terga moderately finely punctate.



**Figure 16.** Dorsal view of the male terminalia of *C. cognatus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** **ARGENTINA – Neuquén:** Neuquén, (-38.929, -68.092), 367m, 16/i/1954, [M.Senkute], 2♀ 1♂, {KUNHM}. **Chubut:** INTA Trevelin site 1, (-43.127, -71.562), 386m, 16/i/2006, [A.Gravel], 1♀ 1♂, {PCYU}; idem, except 23/xii/2006, 2♂♂; idem, except 20/xii/2006, [M.Hollmann], 1♂. INTA Trevelin site 2, (-43.099, -71.542), 481m, 18/i/2007, [M.Gravel], 3♂♂, {PCYU}. **CHILE – Region III:** Chancoquin, (-28.855, -70.291), 1090m, 27/x/1980, [L.Peña], 1♂, {AMNH}. Fundo La Semilla, (-28.255, -69.638), 3355m, 17/xi/2003, [Parker & Irwin], 1♀, {BBSL}. **Region IV:** 7km N of Los Vilos, (-31.849, -71.493), 76m,

11/x/2003, [M.Irwin], 3♀♀11♂♂, {BBSL}; idem, except 11/xii/2003, 2♀♀7♂♂; idem, except 25/xii/2003, [Parker & Irwin], 2♀♀8♂♂. Hacienda Illapel, (-31.631, -71.158), 330m, 16/xi/1963, [Peña], 1♂, {AMNH}. La Serena, (-29.896, -71.253), 15m, 14/i/2000, 1♀, {PCYU}. Ñague, (-31.852, -31.515), 24m, 4/xi/1981, [L.Peña], 1♂, {AMNH}. Quebrada El Arrayán, (-30.104, -70.990), 469m, 21/xi/2003, [Irwin & Parker], 3♀♀, {BBSL}; idem, except 1/ix/2003, 1♂. Vicuña, (-30.022, -70.712), 668m, i/1998, [G.Castillo], 1♂, {AMNH}. **Region V:** El Canelo, (-33.575, -70.445), 865m, 29/xi/1954, [L.Peña], 1♂, {KUNHM}. Mantagua, (-32.937, -71.546), 85m, 30/i/1965, [E.Chiappa], 1♀, {PCYU}. **Region Metropolitana:** El Manzano, (-33.439, -70.634), 489m, 26/i/1984, [L.Peña], 1♀, {AMNH}. Peñalolén, (-33.482, -70.521), 821m, xi/1954, [L.Peña], 1♀, {KUNHM}. Santiago, (-33.433, -70.645), 551m, xii/1951, [L.Peña], 1♂, {KUNHM}. **Region VI:** Rancagua, (-34.187, -70.768), 505m, 1907, [P.Herbst], 1♂, {BBSL}. **Region VII:** Cauquenes, (-33.458, -70.572), 601m, 29/i/1955, [L.Peña], 1♀, {KUNHM}. NW of Laguna del Maule, (-35.550, -70.626), 2569m, 4/i/2009, [L.Packer], 1♂, {PCYU}. Tregualemu, (-35.946, -72.739), 55m, 25/i/1967, [E.Schlinger], 1♂, {EMEC}. **Region VIII:** 6km N of Cobquecura, (-36.084, -72.800), 122m, 29/i/1967, [Irwin & Stange], 1♂, {EMEC}. Las Trancas, (-36.913, -71.500), 1225m, 27/xii/2006, [L.Packer], 1♀, {PCYU}. Queuco, 11/i/1980, [Martinez], 1♂, {PUCV}. **Region IX:** Curacautín, (-38.433, -71.890), 529m, 16/xii/1987, [L.Peña], 1♀, {AMNH}. Loncoche, (-39.369, -72.640), 127m, i/1986, [U.Peña], 1♀1♂, {AMNH}. Lonquimay, (-38.724, -72.601), 117m, i/1994, [L.Peña], 5♂♂, {AMNH}. Marimenuco, (-38.716, -71.100), 1175m, 10/xii/1959, [L.Peña], 3♂♂, {AMNH}.

**Range:** Argentina (Neuquén, Chubut), Chile (Regions III–IX). See also Fig. 3C.

**Biogeographic distribution:** Andean region: Central Chilean sub-region (Coquimban and Santiaguan provinces); Subantarctic sub-region (Maule and Valdivian Forest provinces); Patagonian sub-region (Patagonian province). Central Chilean and western Argentinean species distributed at altitudes of 0–3400m a.s.l.

**DNA barcode:** Available. BOLD: ABA0478 (4♂♂), BOLD BIN: ABA0479 (2♂♂). The distance between the northernmost (Region IV, Chile) and southernmost (Chubut, Argentina) records for BIN BOLD: ABA0478 is about 1250km. Besides, representatives of both BINs occur

sympatrically in Chubut (see Table S1). Distance between BINs: 4.51–6.02. Distance from the nearest neighbour (*C. atripes*): 5.04–8.22%.

**Floral hosts:** Leguminosae – *Trifolium repens* L. (this study).

**Comments:** Common species widely distributed in Chile. According to Toro (1999), *C. cognatus* visits a broad range of plant species, although the records have not been given.

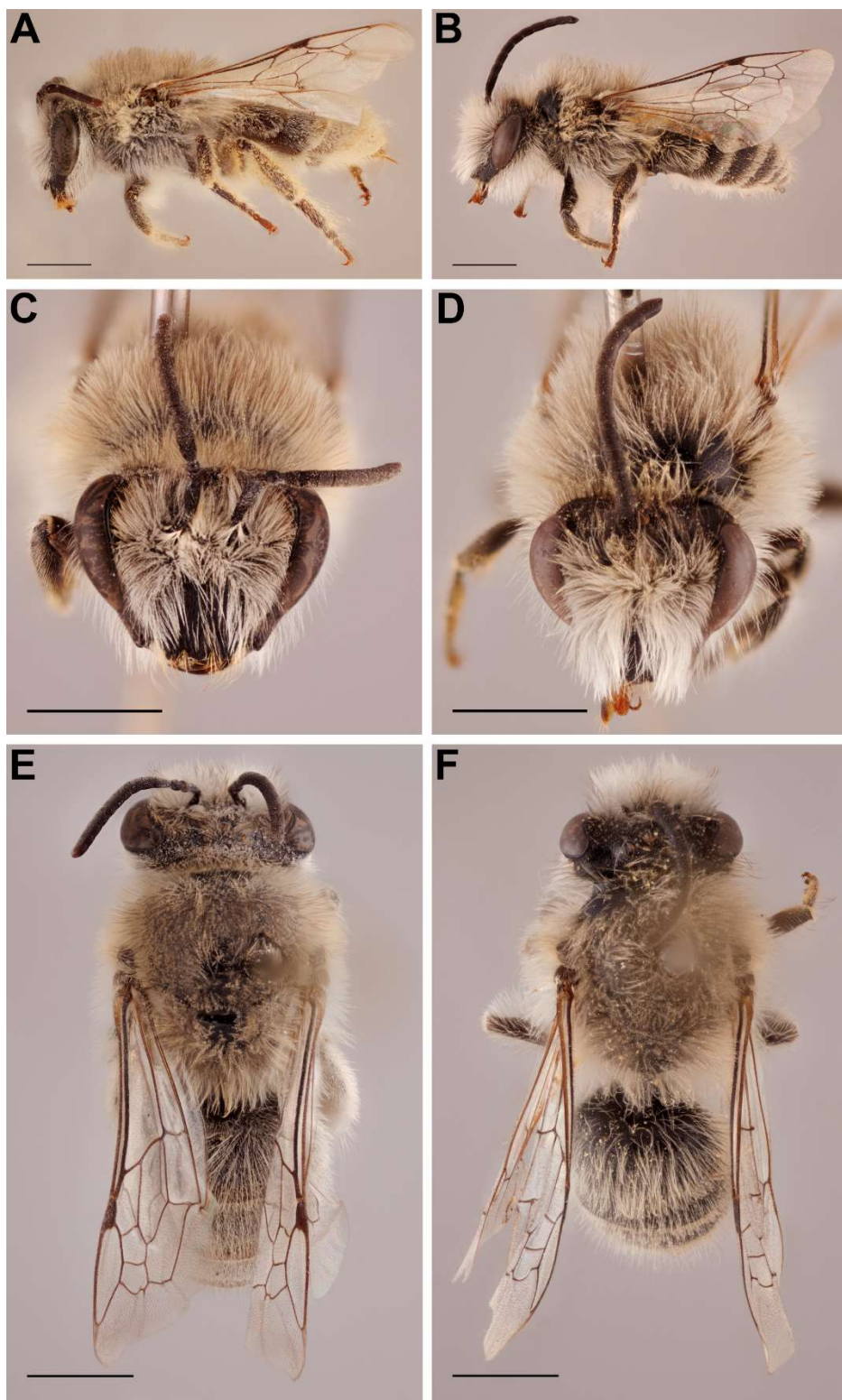
The identity of *C. cognatus* was determined by comparing specimens previously identified by Toro with the original description. As he noted, intraspecific morphological variation in *C. cognatus* is very low throughout its geographic range (Toro 1999). On the other hand, morphologically indistinguishable males – in terms of both external morphology and terminalia – collected in the same area at the same time have been assigned two distinct BINs, suggesting that variation in COI in *C. cognatus* is unusually high.

### ***Colletes coquimbensis* Ferrari, new species**

(Figs. 17A–F)

**Diagnosis:** Females are diagnosable by the combination of clypeus with apicomedial ridge, mesoscutal pubescence with off-white and black hairs intermixed, and posterior hind tibial spur pectinate. Males can be recognized by the combination of malar area  $\sim 1.5\times$  as long as basal depth of mandible, paraocular pubescence with off-white and black hairs intermixed, and marginal zones of T2–T5 covered with pale-yellow appressed hairs.

*Colletes coquimbensis* **n. sp.** is most similar to *C. toroi* **n. sp.** The females, however, can be distinguished from each other by mesoscutum with off-white and black hairs intermixed in *C. coquimbensis* **n. sp.** (mesoscutal pubescence entirely pale-yellow in *C. toroi* **n. sp.**); and the labral median area depressed and margined by ridges in *C. coquimbensis* **n. sp.** (labral median area swollen in *C. toroi* **n. sp.**). The male *C. coquimbensis* **n. sp.** can be readily differentiated from the male *C. toroi* **n. sp.** due to its comparatively shorter malar area,  $\sim 1.5\times$  as long as basal depth of mandible (malar area  $\sim 2\times$  as long as basal depth of mandible in *C. toroi* **n. sp.**).



**Figure 17.** *Colletes coquimbensis* Ferrari, **n. sp.** Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.



**Description:** FEMALE (Figs. 17A, 17C, 17E):

*Dimensions (mm):* Approximate body length 9.3; head width 3.3; head length 2.5; intertegular distance 2.7; forewing length 6.9.

*Colouration:* Black except dark-brown on tegula, wing veins (except vein R of forewing black), stigma, dorsal surface of tarsomeres 4–5, marginal zones of T1–T5, ventrally reflexed lateral areas of T1. Pale-brown on proximal half of tarsal claws. Pale-yellow on tibial spurs, marginal zones of S1–S5. Reddish-brown on distal half of tarsal claws; marked on distal half of mandible.

*Structure:* Labrum medially convex; convexity not margined by ridges. Clypeal mid-longitudinal area neither depressed nor carinate; adjacent lateral area convex; apicomедial ridge present. Malar area ~0.6x as long as basal depth of mandible (23:35). F1 ~1.3x as long as its apical width (31:24). UID:LID (70:65). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.5x as long as metanotum (19:39); metapostnotal pits well-delimited; posterior transverse carina sinuous and interrupted medially. Posteromedial surface of front coxa with short (0.4x MOD) spine. Posterior hind tibial spur pectinate. Hind basitarsus ~3.5x longer than broad (45:14). Outer rami of hind tarsal claws 2.5x as long as inner rami (15:6). Posterolateral area of S6 convex but without carina; marginal zone not depressed.

*Pubescence:* Off-white, plumose, erect, moderately long on vertical surface of clypeal and supraclypeal area, pronotal lobe, metepisternum, ventral margin of mid femur; such hairs long on genal area (except moderately long and mostly suberect on upper 1/2), metanotum, mesepisternum, posteroventral surface of front trochanter and femur, ventral surface of mid and hind trochanters; very long on upper margin of lateral surface of propodeum. Mixed off-white and black, plumose, erect, moderately long hairs on paraocular, frontal and vertexal areas, mesoscutum and scutellum. Pale-yellow, erect, moderately short setae on mandible (except pale-orange), dorsal surface of mid and hind tibiae and basitarsi (except suberect on mid tibia); such hairs moderately long on posterior surface of front tibia, posterior margin of front and mid basitarsi; very long on posterior margin of hind basitarsi. Bright-yellow, suberect, thick setae on ventral surface of mid and hind tarsi; pale-orange, thickest towards distal margin. Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T1–T5 covered with off-white appressed hairs; T1–T2 also with plumose, erect, long hairs

(except slightly shorter on T2); T3–T5 also with pale-yellow and black, erect, moderately long setae (except setae on T3 moderately short and pale-yellow only). S2 with pale-yellow, erect, moderately short hairs, which are branched only apically. Discs of S3–S6 with pale-yellow, erect, moderately short setae restricted to posterior half (except concentrated mid-longitudinally on S6); marginal zones of S2–S5 with a band of plumose, suberect hairs.

*Surface sculpture:* Clypeal mid-longitudinal area densely and moderately finely punctate; adjacent convex area with very sparse punctures, longitudinally striate near depression, smooth elsewhere; lower 1/4 longitudinally striate. Malar area moderately densely and moderately finely punctate on upper 2/3; lower 1/3 substrigulate. Supraclypeal area with a few moderately fine punctures near lower margin; interspaces smooth. Paraocular area punctures crowded throughout; finely punctate above; slightly coarser below. Frontal area densely and moderately coarsely punctate; interspaces rugulose. Vertexal area minutely punctate; interspaces smooth. Mesoscutum moderately sparsely and moderately finely punctate (except sparsely punctate on mid-posterior area); interspaces smooth. Scutellum densely punctate; moderately coarsely punctate on mid 1/3; finer on posterior 1/3; interspaces smooth. Metanotum densely and moderately finely punctate. Mesepisternum densely and coarsely punctate. Metepisternum rugulose above and below; obliquely striate medially. Lateral surface of propodeum finely and sparsely punctate; interspaces rugulose. Upper area of vertical surface of metapostnotum rugose. Metasomal terga sparsely and minutely punctate (except minute punctures on T1 intermingled with fine ones); interspaces smooth throughout. Metasomal sterna moderately finely punctate; densely punctate posterolaterally; sparsely punctate mid-longitudinally and anteriorly; interspaces imbricate throughout.

MALE (Figs. 17B, 17D, 17F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.1; head width 3.1; head length 2.5; intertegular distance 2.6; forewing length 6.8.

*Colouration:* Mandibular reddish-brown spot restricted to distal 1/3. Wing veins pale-brown (except vein R of forewing black).

*Structure:* Clypeal mid-longitudinal area evenly broadly depressed; depression shallow for upper 2/4, deeper just below; apicomедial ridge absent. Malar area ~1.5x as long as basal

depth of mandible (42:27). F1 slightly longer than its apical width (24:22). UID:LID (67:60). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded. Horizontal surface of metapostnotum ~0.7x as long as metanotum (22:33); posterior transverse carina complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.7x longer than broad (41:11). Outer rami of hind tarsal claws ~2.7x as long as inner rami (22:8). Posterolateral area of S6 flat. S7, S8 and genital capsule as in Figs. 18A, 18B, 18C, respectively.

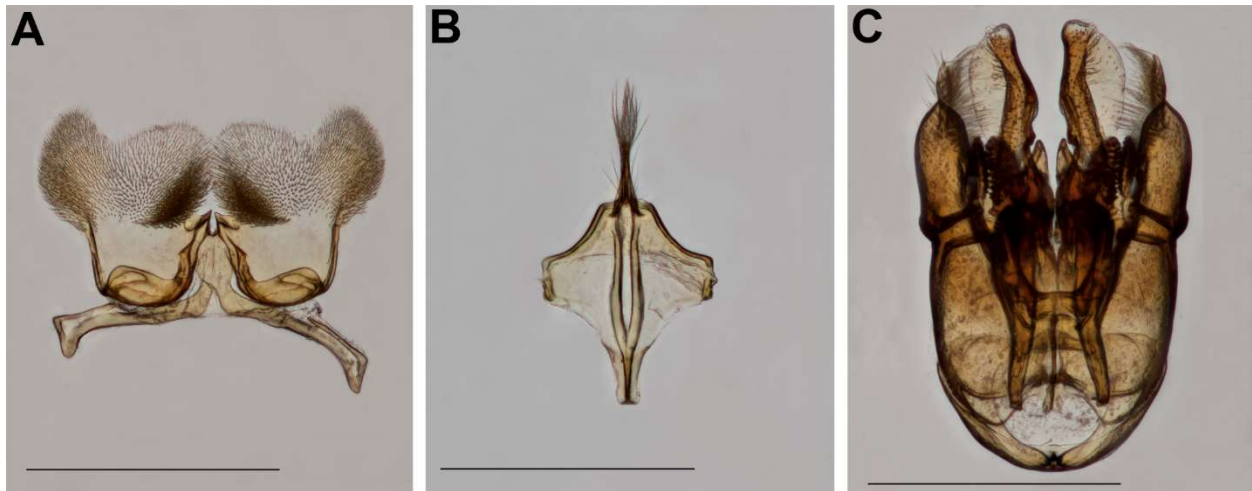
*Pubescence*: Pale-yellow hairs on interantennal area intermingled with black ones. Genal pubescence evenly long and erect. Appressed hairs on metasoma restricted to marginal zones. Setae on discs of S3–S6 more evenly distributed.

*Surface sculpture*: Clypeal mid-longitudinal area punctures crowded. Supraclypeal punctation more evenly distributed. Paraocular area only densely punctate. Lateral surface of propodeum with rugose interspaces. Metasomal terga finely and moderately densely punctate throughout.

**Type material:** *Holotype* ♀ – “CHILE: Region IV; La Mercedes; IX-15-2010; L. Packer”. “B10006-B12; Bees of Chile 119”. “HOLOTYPE; *Colletes coquimbensis* ♀; Ferrari, new species”. {PCYU}.

*Paratypes*: **CHILE – Region IV**: 4km S of Pisco Elqui, (-30.162, -70.491), 1362m, 26/x/1992, [Rozen, Sharkov & Snyder], 8♀♀, {AMNH}. 6km S of Pisco Elqui, (-30.180, -70.485), 1464m, 30/x/1992, [J.Rozen], 3♀♀, {AMNH}. 7km S of Pisco Elqui, (-30.189, -70.483), 1471m, 8/x/1994, [Rozen, Quinter & Ascher], 24♀♀, {AMNH}; idem, except 6/x/1994, 2♀♀. Alcohuaz, (-30.115, -70.491), 1190m, 2/xi/1986, [L.Peña], 1♀, {AMNH}. Las Mercedes, (-29.935, -70.537), 926m, 15/ix/2010, [L.Packer], 1♀, {PCYU}. Las Placetas, (-30.170, -70.599), 3115m, 14/x/2001, [Rozen, Ugarte & Espina], 4♀♀5♂♂, {AMNH}; idem, except 15/x/2001, 2♂♂. Near Pisco Elqui, 1/xi/2000, [J.Rozen], 5♀♀, {AMNH}; idem, except 2/xi/2000, 4♀♀; idem, except 12/xi/2000, 1♀.

**Range**: Chile (Region IV). See also Fig. 19A.



**Figure 18.** Dorsal view of the male terminalia of *C. coquimbensis* **n. sp.** (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

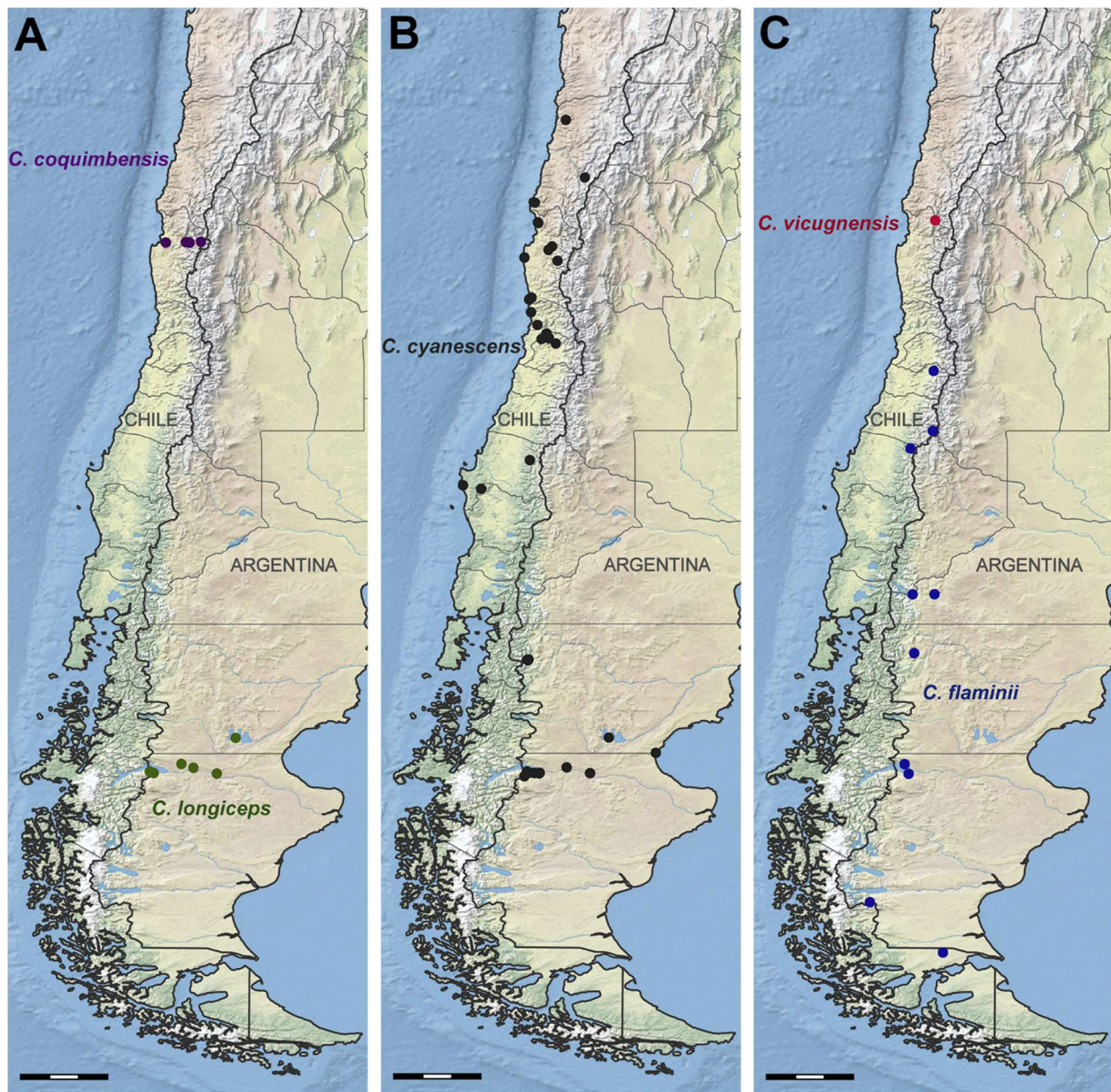
**Biogeographic distribution:** Andean region: Central Chilean sub-region (Coquimban province). Central Chilean species distributed at altitudes of 900–3200m a.s.l.

**DNA barcode:** Available. BOLD: AAO3472 (2♀♀2♂♂). Distance from the nearest neighbour (*C. cognatus*): 7.32–8.84%.

**Floral hosts:** Unknown.

**Etymology:** *Colletes coquimbensis* **n. sp.** is a reference to the fact that the species has so far been found only in the Chilean Region IV (Coquimbo).

**Comments:** All specimens available to me were collected in Region IV, which suggests that *C. coquimbensis* **n. sp.** may have a restricted distribution in Chile. The species also appears to be uncommon within its range.



**Figure 19.** Geographic distribution by *Colletes* species. (A) *C. coquimbensis* **n. sp.** and *C. longiceps*; (B) *C. cyanescens*; (C) *C. vicugnensis* and *C. flaminii*. Scale bars approximately 300 km.

According to the AMNH's records, four female specimens caught by Rozen near Pisco Elqui (Region IV) on November 2000 were collected along with *Isepeolus luctuosus* (Spinola, 1851). As no other *Colletes* species was collected there on the same date, it may be sensible to consider *I. luctuosus* as a presumable cleptoparasite of *C. coquimbensis* **n. sp.** In fact, Claude-



Joseph (1926) had associated *I. luctuosus* with three *Colletes* species: *C. sulcatus* (as *C. araucariae*), *C. cyaniventris* (as *C. cyanescens*) and *C. lucens* (as *C. laticeps*). Perhaps, the specimens identified by him as *C. sulcatus* actually belong to the species described here as new.

***Colletes cyanescens* (Haliday, 1836)**

(Figs. 20A–F)

*Andrena cyanescens* Haliday, 1836: 321.

Lectotype ♀ (examined). {NHM}. [hereby designated]

*Colletes semi-nitida* Spinola, 1851: 225; Vachal 1909: 54. [new synonymy]

Syntype ♀ (not examined). {MRSN}.

*Colletes cyanescens*; Smith 1853: 5; Dalla Torre 1896: 40; Cockerell 1904: 257, 1917b: 478; Claude-Joseph 1926: 128; Jaffuel & Pirion 1926: 364; Gazulla & Ruiz 1928: 300; Ruiz 1944: 210; Stephen 1954: 161; Moure 1956: 203; Roig-Alsina 1991: 259; Toro 1986: 122, 1999: 27; Moure & Urban 2002: 7; Moure *et al.* 2007: 680; Montalva & Ruz 2010: 21; Ascher & Pickering 2017.

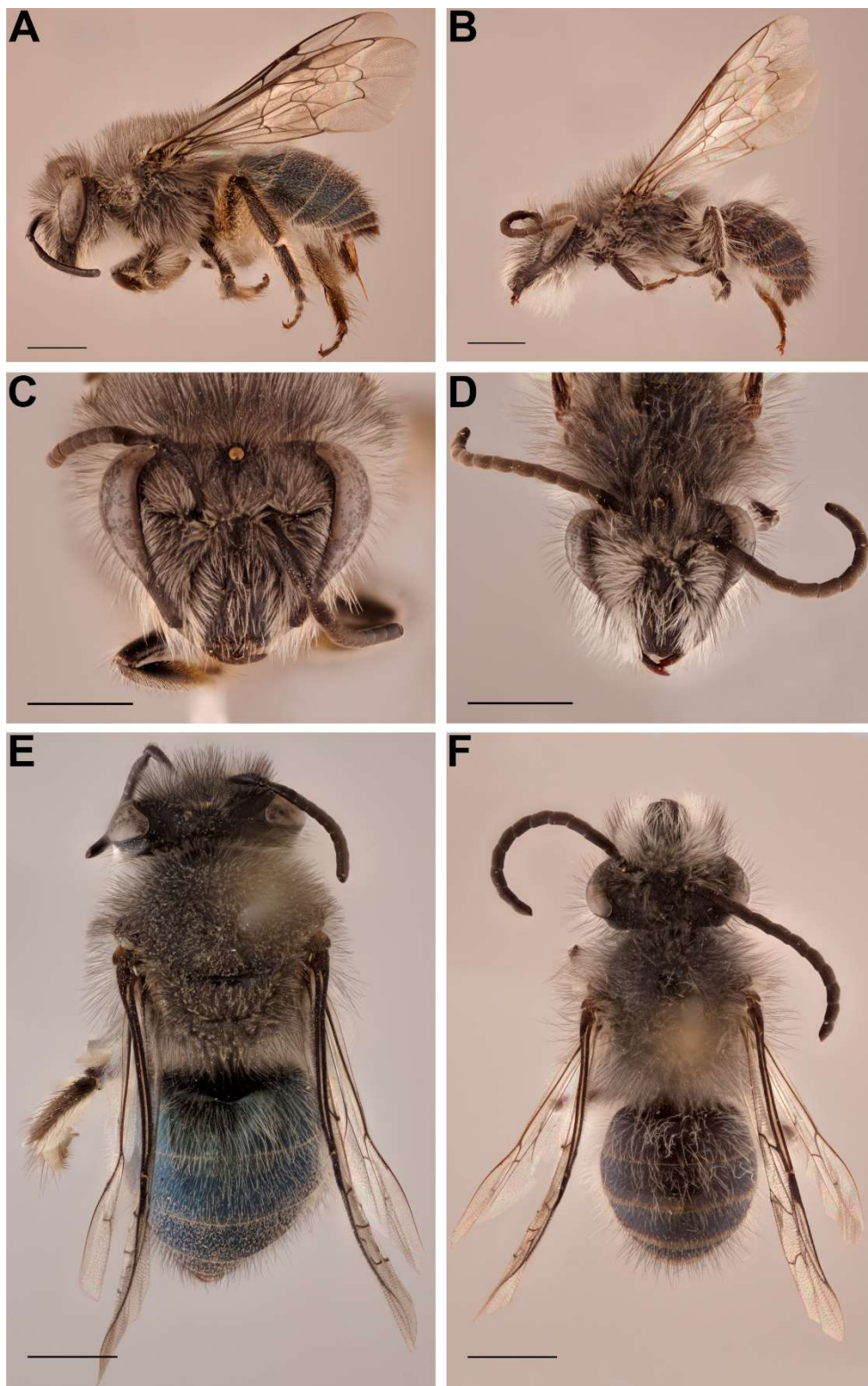
*Colletes seminitidus*; Dalla Torre 1896: 44; Claude-Joseph 1926: 130; Jaffuel & Pirion 1926: 364; Gazulla & Ruiz 1928: 300; Ruiz 1944: 217; Roig-Alsina 1991: 259; Toro 1999: 30; Moure & Urban 2002: 20; Vázquez & Simberloff 2002: 621; Packer *et al.* 2005: 197; Zayed *et al.* 2005: 1018; Moure *et al.* 2007: 687; Almeida & Danforth 2009: 293; Kuhlmann *et al.* 2009: 296; Montalva & Ruz 2010: 22; Almeida *et al.* 2011: 7; Ascher & Pickering 2017.

*Colletes viridans* Vachal, 1909: 55.

Lectotype ♀ (examined). {MNHP}. [hereby designated]

*Colletes seminitida*; Rojas & Toro 1993: 86.

**Diagnosis:** The combination of clypeal mid-longitudinal area depressed and not carinate, mesosomal pubescence with off-white and black hairs intermixed, and metasomal terga metallic greenish-blue is sufficient to diagnose both sexes of *C. cyanescens*.



**Figure 20.** *Colletes cyanescens* (Haliday, 1836). Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

*Colletes cyanescens* is most similar to *C. musculus*, however, the former is different by having metallic greenish-blue T1–T5 (T1–T5 opaque dark-blue in *C. musculus*); and marginal zones of T1–T4 with the same colour as discs (marginal zones of T1–T4 dark-brown, contrasting with the opaque dark-blue discs, in *C. musculus*).

**Redescription:** FEMALE (Figs. 20A, 20C, 20E):

*Dimensions (mm):* Approximate body length 9.8–11.2; head width 3.7–4.2; head length 2.8–3.2; intertegular distance 2.9–3.4; forewing length 8.2–8.9.

*Colouration:* Black except metallic greenish-blue on T1–T5 (T5 also with some golden hues). Metallic dark-blue on discs of S2–S5. Dark-brown on tegula, wing veins (except basal veins of forewing black), stigma, distal 1/5 of dorsal surface of distitarsi, ventrally reflexed lateral areas of T1. Pale-brown on proximal 1/3 of tarsal claws, posterior margin of ventrally reflexed lateral areas of T3–T5, marginal zones of metasomal sterna. Reddish-brown on distal 2/3 of tarsal claws; marked on distal 1/4 of mandible. Pale-yellow on tibial spurs.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area evenly deeply depressed on upper 3/4; depression narrow (0.4x MOD) on upper 1/4, broader (0.7x MOD) on middle 2/4; adjacent lateral area convex; apicomedial ridge absent. Malar area ~1.2x as long as basal depth of mandible (35:28). F1 ~1.6x as long as its apical width (26:16). UID:LID (77:80). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum ~0.25x as long as metanotum (13:50); metapostnotal pits well-delimited; posterior transverse carina straight and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus 3.5x longer than broad (56:16). Outer rami of hind tarsal claws 1.8x as long as inner rami (18:10). Posterolateral area of S6 convex and lacking carina; marginal zone depressed.

*Pubescence:* Mixed off-white and black, plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, paraocular and interantennal areas, mesoscutum, scutellum, metepisternum; such hairs long on frontal and vertexal areas, metanotum, mesepisternum; very long on upper margin of lateral surface of propodeum. On genal area, mostly off-white (except area adjacently to outer margin of eye with black hairs) and moderately short (except very long towards proboscis fossa). Off-white only, plumose, erect, moderately long on anterior surface

of mid trochanter, ventral margin of mid femur, T1, S1; such hairs short on T2. Fulvous, erect, moderately short setae on dorsal surface of mid and hind basitarsi and hind tibia; such hairs moderately long on mandible, posterior margin of basitarsi (except long on hind one). Pale-yellow, suberect, short setae on dorsal surface of front and mid tibiae; thicker setae on ventral surface of mid and hind tarsi; fulvous, thickest towards distal margin. Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T2–T5 covered with off-white, sparse appressed hairs (on T2 restricted laterally and posteriorly); T3–T5 also with black, erect, moderately long setae (except short on T3). S2 with pale-yellow, erect, moderately short hairs, which are branched only apically. Discs of S3–S6 with pale-yellow, suberect, short setae; marginal zones with a line of plumose, erect, moderately short hairs.

*Surface sculpture:* Clypeal mid-longitudinal depression finely and moderately sparsely punctate (interspaces imbricate); adjacent convex area with moderately fine punctures near depression (interspaces smooth); lower 1/4 longitudinally striate. Malar area rugose. Supraclypeal area imbricate. Paraocular area densely and moderately finely punctate below; moderately densely and finely punctate above; interspaces imbricate throughout. Frontal area moderately densely and moderately finely punctate; interspaces rugose. Vertexal area with minute and fine punctures intermingled near eye (interspaces smooth); densely punctate near ocellus (interspaces rugose). Mesosomal and metasomal interspaces imbricate throughout. Mesoscutum and metanotum moderately coarsely and moderately sparsely punctate (except sparsely punctate on mesoscutal mid-posterior area). Scutellum coarsely and moderately densely punctate. Mesepisternum coarsely and densely punctate anteriorly to episternal groove and near scrobe; moderately densely punctate elsewhere. Metepisternum rugose above and below; obliquely striate medially. Lateral surface of propodeum imbricate. Upper area of vertical surface of metapostnotum transversely striate medially. Metasomal terga minutely and moderately sparsely punctate (except sparsely punctate on T1). Metasomal sterna finely and densely punctate.

MALE (Figs. 20B, 20D, 20F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.1–8.9; head width 3.4–3.7; head length 2.8–3.0; intertegular distance 2.3–2.8; forewing length 7.6–8.2.

*Colouration:* Dark-brown on vein C of forewing, dorsal surface of tarsi, S6 laterally. Pale-brown on mid-longitudinal band of S2–S5.

*Structure:* Clypeal mid-longitudinal area deeply depressed on upper 3/5, depression shallow on lower 2/5; depression narrowest (0.5x MOD) on upper 1/3, broader (0.8x MOD) on middle 1/3; broadest (=MOD) on lower 1/3. Malar area ~2.1x as long as basal depth of mandible (64:30). F1 ~1.3x as long as its apical width (38:28). UID:LID (75:70). Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.3x as long as metanotum (14:46); posterior transverse carina sinuous. Hind basitarsus ~4x longer than broad (54:14). Outer rami of hind tarsal claws ~1.6x as long as inner rami (22:14). Posterolateral area of S6 flat carina; marginal zone not depressed. S7, S8 and genital capsule as in Figs. 21A, 21B, 21C, respectively.

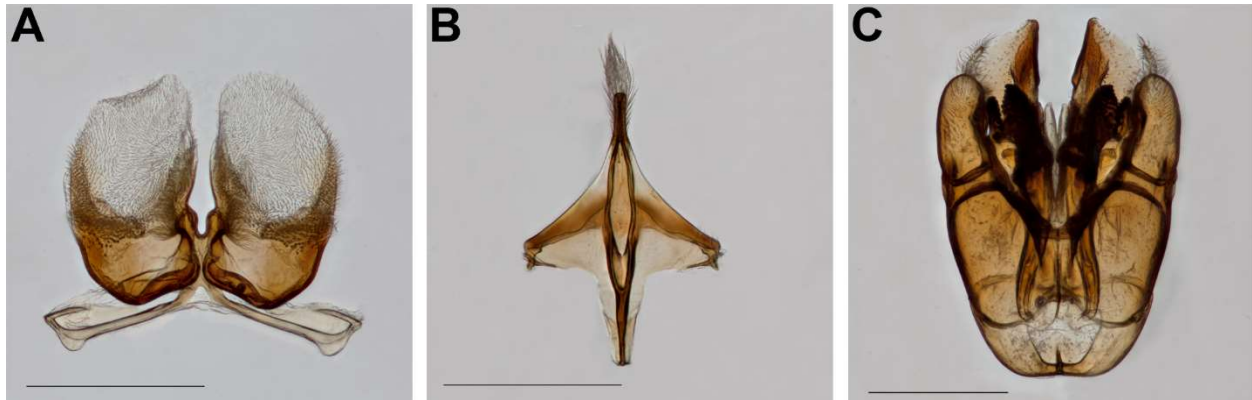
*Pubescence:* Lateral slopes of clypeus with off-white hairs only. Legs with pale-yellow setae. Plumose hairs on T2 only slightly shorter than those on T1; appressed hairs restricted to marginal zone. Discs of S2–S5 covered with minute setae.

*Surface sculpture:* Clypeal convex area smooth throughout. Punctuation on frontal area difficult to discern from the overall rugose integument. Interspaces on vertexal area imbricate near eye. Scutellum moderately coarsely punctate. Mesepisternum moderately densely punctate. Upper area of vertical surface of metapostnotum rugose medially. T2–T5 finely punctate.

**Material studied:** *Primary type specimens:* Lectotype ♀ of *Andrena cyanescens* – “Type”. “B. M. TYPE; HYM.; 17.a535”. “*Andrena; cyanescens* Hal.”. “SYN-; TYPE”. “63; 43”. “♀; Chil”. “*albopilosus* Spinola.”. “Collected by Capt’n; King: presented by the; Linnean Society; BMNH (E) 1863-43”. “LECTOTYPE; *Andrena cyanescens* ♀; Haliday, 1836; designated R. Ferrari, 2017”. {NHM}. [hereby designated]. Lectotype ♀ of *C. viridans* – “CHILE; CONCEPC; 22.10.1904; P. HERBST”. “MUSEUM PARIS; Coll. J. VACHAL 1911”. “LECTOTYPE; *Colletes viridans* ♀; Vachal, 1909; designated R. Ferrari, 2017”. [hereby designated]. {MNHP}.

*Secondary type specimens:* Paralectotypes ♀♀ and ♂♂ of *C. viridans* – **CHILE** – 1863, 1♂, {MNHP}; idem, except no date indicated, 2♀♀. **Region V:** Quillota, 1♀1♂, {MNHP}. **Region VIII:** Ñuble, 25/ix/1900, 1♂, {MNHP}.





**Figure 21.** Dorsal view of the male terminalia of *C. cyanescens*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Additional specimens:* **ARGENTINA – Chubut:** 8km N of Sarmiento, (-45.512, -69.057), 265m, 26/xi/2003, [L.Packer], 3♀♀, {PCYU}. 8km S of Rada Tilly, (-45.984, -67.605), 35m, 24/xi/2003, 1♀, {PCYU}. INTA Trevelin site 1, (-43.127, -71.562), 386m, 24/x/2005, [A.Gravel], 1♀1♂, {PCYU}; idem, except 24/x/2006, 1♂; idem, except 3/xi/2006, [M.Gravel], 2♂♂. INTA Trevelin site 2, (-43.099, -71.542), 481m, 26/x/2005, [A.Gravel], 1♀, {PCYU}; idem, except 2/xii/2005, [M.Hollmann], 3♀♀; idem, except 25/x/2006, [M.Gravel], 1♂; idem, except 8/xi/2006, [M.Gravel], 4♂♂. INTA Trevelin site 3, (-43.114, -71.590), 688m, 17/xi/2006, [A.Gravel], 2♂♂, {PCYU}. INTA Trevelin site 4, (-43.100, -71.552), 539m, 1/xi/2005, [A.Gravel], 18♂♂, {PCYU}; idem, except 9/xi/2005, [M.Hollmann], 5♂♂; idem, except 2/xi/2006, [M.Gravel], 6♂♂; idem, except 22/xi/2006, [M.Gravel], 2♂♂. **Santa Cruz:** 0.5km E of Los Antiguos, (-46.558, -71.591), 232m, 17/xi/2003, [L.Packer], 11♀♀4♂♂, {PCYU}; idem, except 16/xi/2003, 1♀. 5km E of Los Antiguos, (-46.598, -71.493), 308m, 17/xi/2003, [L.Packer], 1♂, {PCYU}. 20km E of Los Antiguos, (-46.609, -71.357), 229m, 17/xi/2003, [L.Packer], 1♂, {PCYU}. 23km W of Las Heras, (-46.613, -69.639), 395m, 16/xi/2003, [L.Packer], 6♀♀, {PCYU}. 25km S of Los Antiguos, (-46.710, -71.673), 656m, 22/xi/2003, [L.Packer], 4♂♂, {PCYU}. 35km E of Los Antiguos, (-46.601, -71.197), 244m, 17/xi/2003, [L.Packer], 2♀♀1♂, {PCYU}. 39km E of Los Antiguos, (-46.601, -71.129), 387m, 16/xi/2003, [L.Packer], 1♀, {PCYU}. 43km E of Perito Moreno, (-46.434, -70.364), 534m, 16/xi/2003, [L.Packer], 1♀, {PCYU}. Cueva de Los Manos, (-47.158, -70.660), 545m, 20/xi/2003, [L.Packer], 1♀. {PCYU}. **CHILE – Region III:** Chañar de Aceituno, (-28.953, -71.347), 276m,

18/ix/2003, [A.Ugarte], 2♀♀1♂, {PCYU}. Highway C-13 km 15, (-26.395, -70.388), 322m, 16/ix/2010, [L.Packer], 4♀♀6♂♂, {PCYU}. Road to Mina Caserones, (-28.174, -69.803), 1849m, 30/ix/2013, [L.Packer], 1♀, {PCYU}. **Region IV:** 1.1km S of Tololo, (-30.305, -70.815), 1555m, 11/x/2009, [J.Gibbs], 2♀♀, {PCYU}. Cuesta Buenos Aires, (-29.562, -71.253), 517m, 13/x/2013, [Postlethwaite & Monckton], 1♀, {PCYU}. Las Mercedes, (-29.935, -70.537), 926m, 15/ix/2010, [L.Packer], 1♀, {PCYU}. Los Lobos, (-31.922, -71.518), 21m, 11/v/2010, [Packer & Fraser], 1♀, {PCYU}. Los Molles, (-30.749, -70.648), 1179m, 12/x/2013, [S.Monckton], 1♀, {PCYU}. Los Vilos, (-31.918, -71.511), 18m, 25/ix/1966, [E.Schlinger], 1♀, {EMEC}. N of Los Hornos, (-29.581, -71.241), 402m, 8/x/2002, [Grixti & Zayed], 3♀♀, {PCYU}; idem, except 9/x/2002, 1♀; idem, except 25/ix/2002, 1♀; idem, except 7/x/2002, 1♀. Parque Nacional Fray Jorge, (-30.637, -71.597), 259m, 13/x/2000, [L.Packer], 9♀♀, {PCYU}; idem, except 7/x/2001, 1♀; idem, except 20/x/2001, [Packer & Fraser], 3♀♀; idem, except 11/x/2002, [Grixti & Zayed], 2♀♀; idem, except 12/x/2002, [Grixti & Zayed], 9♀♀; idem, except 10/x/2009, [J.Gibbs], 2♀♀1♂. Puente Samo Alto, (-30.413, -70.927), 643m, 13/x/2002, [Grixti & Zayed], 2♀♀, {PCYU}. Punta de Lobos, (-31.948, -71.524), 16m, 11/x/2013, [S.Monckton], 1♀, {PCYU}. S of Los Vilos, (-31.931, -71.513), 15m, 11/x/2013, [S.Monckton], 3♀♀, {PCYU}. **Region V:** Colliguay, (-33.138, -71.149), 502m, 6/x/2000, [L.Packer], 3♀♀, {PCYU}; idem, except 4/x/2001, [Packer & Fraser], 2♀♀1♂. Nogales, (-32.733, -71.266), 267m, 1/viii/1966, [E.Schlinger], 1♂, {EMEC}. **Region Metropolitana:** 7km S of Tiltill, (-33.145, -70.913), 550m, 28/x/2002, [Grixti & Zayed], 1♀, {PCYU}. 10km NW of Tiltill, (-33.000, -70.983), 1090m, 11/x/2010, [Almeida & Packer], 1♀1♂, {RPSP}. Caleu, (-33.008, -70.996), 1201m, 26/x/2010, [L.Packer], 1♂, {PCYU}; idem, except 3/x/2000, 1♀; idem, except 6/x/2010, [Packer & Fraser], 1♂; idem, except 8/xi/1997, 5♀♀. La Vega, 3/x/2000, [L.Packer], 4♂♂, {PCYU}. Las Canteras, (-33.308, -70.699), 531m, 9/x/2013, [S.Monckton], 1♀, {PCYU}. Pichicuy, (-32.341, -71.466), 42m, 17/x/2002, [Grixti & Zayed], 1♀, {PCYU}; idem, except 9/x/2000, [L.Packer], 1♀. **Region VIII:** 20km W of Caramavida, (-37.699, -73.575), 173m, 13/i/1967, [E.Schlinger], 1♂, {EMEC}. Las Trancas, (-36.913, -71.500), 1225m, 17/xii/1976, [Peck & Howden], 1♀6♂♂, {KUNHM}. **Region IX:** Parque Nacional Nahuelbuta, (-37.791, -73.001), 1325m, 27/xi/1997, [L.Packer], 1♀, {PCYU}; idem, except 31/x/2001, [Packer & Fraser], 4♀♀11♂♂.

**Range:** Argentina (Chubut, Santa Cruz), Chile (Regions III–IX). See also Fig. 19B.

**Biogeographic distribution:** Andean region: Central Chilean sub-region (Coquimban and Santiaguan provinces); Subantarctic sub-region (Maule province); Patagonian sub-region (Patagonian province). Central Chilean and southern Argentinean species distributed at altitudes of 0–1900m a.s.l.

**DNA barcode:** Available. BOLD: ABY2997 (8♀♀13♂♂), BOLD: ACW1675 (1♀), BOLD BIN: AAC8707 (2♀♀). Barcoded specimens cover the latitudinal range of the species fairly well, including both northernmost (Region III, Chile) and southernmost (Santa Cruz, Argentina) records. The distances between the northernmost and southernmost records for BINs BOLD: AAC8707 and BOLD:ABY2997 are approximately 920km and 2240km, respectively; representatives of both occur sympatrically in Region IV. Females of BINs ACW1675 and AAC8707 are sympatric (see Table S1). Distance amongst BINs: 0.84–3.64%. Distance from the nearest neighbour (*C. musculus*): 1.73–4.04%.

**Floral hosts:** Anacardiaceae – *Schinus patagonica* (Phil.) I. M. Johnst. ex Cabrera (this study). Celastraceae – *Maytenus boaria* Molina (Claude-Joseph 1926). Compositae – *Taraxacum campylodes* G. E. Haglund (this study). Elaeocarpaceae – *Aristotelia chilensis* (Molina) Stuntz [Claude-Joseph 1926; Toro 1999 (as *Aristotelia macqui* L’Hér)]. Grossulariaceae – *Ribes magellanicum* Poir. (this study). Leguminosae – *Cytisus scoparius* (L.) Link (this study). Loasaceae – *Loasa tricolor* Ker Gawl. (this study). Proteaceae – *Lomatia hirsuta* (Lam.) Diels (this study). Rhamnaceae – *Colletia spinosissima* J. F. Gmel [Claude-Joseph 1926; Toro 1999 (as *Colletia ferox* Gillies & Hook)]; *Retanilla trinervia* (Gillies & Hook.) Hook. & Arn. [Toro 1999 (as *Trevoa trinervis* Miers)]; *Talguenea costata* Miers (Claude-Joseph 1926). Zygophyllaceae – *Porlieria hygrometrica* Ruiz & Pav. (Claude-Joseph 1926).

**Comments:** *Colletes cyanescens* is probably the most common species of the genus found in central Chile, where it visits a wide range of plant species (at least 12 species from 10 different families).

The interpretation of *C. cyanescens*' identity by this study is different from that by various previous authors (see synonymy list, above). Examination of the female lectotype revealed that the actual *C. cyanescens* matches the species that has been traditionally identified as *C. seminitidus* by numerous bee taxonomists. Therefore, I am herein proposing that *C. seminitidus* is a junior synonym of *C. cyanescens*, even though I have not examined the type specimen of the former. In addition to the vast, previously identified material that I had access to, this synonymy is also supported by the fact that Spinola's description of *C. seminitidus* fully matches the lectotype of *C. cyanescens*. Toro's proposition of synonymy involving *C. viridans* (type material studied) and *C. seminitidus* further endorses the nomenclatural act made in this study.

As will be seen below, the species commonly acknowledged as *C. cyanescens* is herein treated under the name *C. cyaniventris*.

***Colletes cyaniventris* Spinola, 1851, new status**

(Figs. 22A–F)

*Colletes cyani-ventris* Spinola, 1851: 224.

Lectotype ♀ (not examined) designated by Moure & Urban (2002: 7). {MRSN}.

*Colletes cyaniventris*; Vachal 1909: 54; Ducke 1912: 81; Friese 1910: 645, 1912: 366; Toro 1986: 122; Rojas & Toro 1993: 86.

*Colletes atripilis* Vachal, 1909: 55. [new synonymy]

Lectotype ♂ (examined) designated by Moure & Urban (2002: 8). {MNHP}.

**Diagnosis:** *Colletes cyaniventris* is unique among the Chilean species of the genus in having the following combination of characteristics: body size with 13/10mm (♀/♂) in length, clypeal mid-longitudinal area not carinate, mesosoma with black hairs only, and metasoma metallic blue.

*Colletes cyaniventris* is most similar to *C. cyanescens* and *C. musculus*, but it can be differentiated from those species by the mesepisternum with smooth interspaces (interspaces imbricate in both *C. cyanescens* and *C. musculus*).



**Figure 22.** *Colletes cyaniventris* Spinola, 1851. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.



**Redescription:** FEMALE (Figs. 22A, 22C, 22E):

*Dimensions (mm):* Approximate body length 11.0–13.5; head width 3.6–4.3; head length 2.8–3.2; intertegular distance 3.3–3.7; forewing length 8.4–9.5.

*Colouration:* Black except metallic blue on metasoma (except T6 black and S6 dark-brown), with purplish and greenish reflections on metasomal sterna. Reddish-brown on distal half of tarsal claws; marked on distal 1/3 of mandible. Dark-brown on anterior surface of front and mid femora, ventral surface of hind femur, dorsal surface of tarsi, wing veins (except veins C and R of forewing black), stigma. Pale-brown on anterior half of tarsal claws.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area deeply and narrowly (0.3x MOD) on upper half; adjacent lateral area convex; apicomedial ridge absent. Malar area about half as long as basal depth of mandible (34:65). F1 ~1.2x as long as its apical width (37:31). UID:LID (77:75). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded. Horizontal surface of metapostnotum 0.3x as long as metanotum (25:84); metapostnotal pits well-delimited; posterior transverse carina straight and interrupted medially. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3x longer than broad (53:18). Outer rami of hind tarsal claws ~2.1x as long as inner rami (34:16). Posterolateral area of S6 convex and bearing thick stria; marginal zone not depressed.

*Pubescence:* Black, plumose, erect, moderately long on lateral slopes of supraclypeal area, genal area (except long towards proboscis fossa), mesoscutum, scutellum, ventral surface of front and mid coxae, T1 laterally; such hairs long on paraocular, frontal and vertexal areas, metanotum, mesepisternum, metepisternum, central area of lateral surface of propodeum, posteroventral surface of front trochanter and femur, anteroventral surface of mid trochanter, ventral margin of mid femur, disc of T1; very long on upper margin of lateral surface of propodeum, ventral surface of hind coxa and trochanter, S1. Black, erect, moderately short setae on dorsal surface of front tibia and tarsus, T3, T4 laterally, S3–S6; moderately long on mandible, posterior surface of front coxa, posterior surface of front tibia and basitarsus, dorsal surface of mid and hind tibiae and basitarsi. Black, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. Fulvous, suberect, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. S2 with mixed black, erect, moderately short hairs, which are branched only apically, and long, plumose hairs.

*Surface sculpture:* Clypeal convex area densely and coarsely punctate; mid-longitudinal depression with fine punctures; lower 1/3 longitudinally striate. Malar area densely and moderately finely punctate on upper half; substrigulate on lower half. Supraclypeal area imbricate. Lower paraocular area punctures crowded and moderately coarse; interspaces smooth. Upper paraocular area densely and moderately finely punctate; interspaces rugulose. Frontal area densely and moderately coarsely punctate; interspaces rugulose and dull. Vertexal area with minute punctures intermingled with fine ones; interspaces smooth and shiny. Mesoscutum punctures crowded and moderately coarse (except densely punctate mid-posteriorly); interspaces smooth throughout. Scutellum densely and moderately coarsely punctate; interspaces imbricate. Metanotum punctures crowded and moderately fine; interspaces smooth. Mesepisternum punctures crowded and coarse; interspaces smooth and shiny. Metepisternum rugose above; obliquely striate medially; rugulose below. Lateral surface of propodeum with very sparse coarse punctures; interspaces imbricate. Upper area of vertical surface of metapostnotum smooth medially. Metasoma sparsely and minutely punctate on terga; finely and moderately sparsely punctate; interspaces imbricate but shiny.

MALE (Figs. 22B, 22D, 22F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.5–11.1; head width 3.0–3.5; head length 2.6–2.9; intertegular distance 2.8–3.3; forewing length 8.1–8.8.

*Colouration:* Tibial spurs dark-brown. T1–T2 with purplish reflections. Dorsal surface of mid and hind trochanters dark-brown.

*Structure:* Labral mid depression not margined by ridges. Malar area as long as basal depth of mandible (46:46). F1 ~1.2x as long as its apical width (26:21). UID:LID (70:60). Genal area concave behind upper summit of compound eyes in lateral view. Horizontal surface of metapostnotum ~0.35x as long as metanotum (25:70); metapostnotal pits poorly-delimited; posterior transverse carina low. Hind basitarsus ~2.8x longer than broad (53:19). Outer rami of hind tarsal claws ~1.4x as long as inner rami (26:18). Posterolateral area of S6 flat and lacking thick stria. S7, S8 and genital capsule as in Figs. 23A, 23B, 24C, respectively.

*Pubescence:* Off-white on lateral slopes of clypeus and supraclypeal area, interantennal area. Off-white and black hairs intermixed on proboscis fossa, pronotal lobe, mesoscutum,

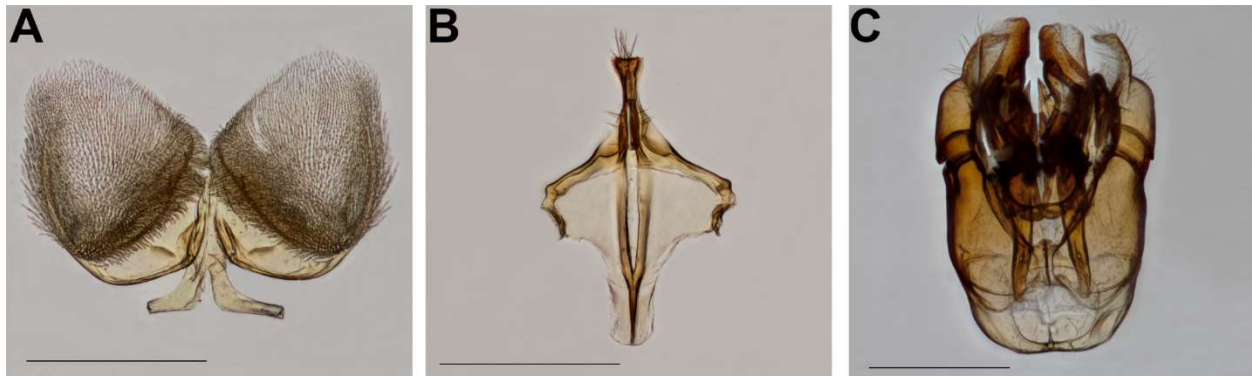
scutellum, metanotum. S2 with plumose hairs only. Marginal zones of S2–S5 with a row of off-white, plumose, erect, moderately long hairs.

*Surface sculpture:* Clypeal mid-longitudinal area finely punctate. Supraclypeal and upper paraocular areas, scutellar anterior 2/3, metepisternum below, lateral surface of propodeum, metasomal terga with smooth interspaces. Sparsely punctate area on mesoscutum larger; densely and moderately finely punctate elsewhere. Scutellar interspaces rugulose on posterior 1/3. Mesepisternum moderately sparsely and moderately coarsely punctate. Lateral surface of propodeum finely and sparsely punctate. Metasomal terga finely and moderately sparsely punctate.

**Material studied:** *Primary type specimen:* Lectotype ♂ of *C. atripilis* – “Chili; 63”. “MUSEUM PARIS; Chili; COLL. O. SICHEL 1867”. “Colletes ♂; atripilis; Vach”. “TYPE”. “SYNTYPE”. “LECTOTYPE; Colletes atripilis ♂; Vachal, 1909; labelled R. Ferrari, 2017”. {MNHP}.

*Secondary type specimens:* Paralectotypes ♀♀ and ♂♂ of *C. atripilis* – **CHILE** – 1863, 4♀3♂, {MNHP}.

*Additional specimens:* **CHILE – Region V:** Cerro El Roble, (-33.007, -71.020), 1566m, 1/i/2009, [L.Packer], 1♀1♂, {PCYU}. El Melón, (-32.688, -71.208), 246m, x/1998, [R.Madariaga], 2♀♀, {AMNH}. **Region Metropolitana:** Caleu, (-32.997, -70.977), 1055m, 1/i/2009, [L.Packer], 4♀♀, {PCYU}. El Manzano, (-33.439, -70.634), 489m, 8/xii/1945, [L.Peña], 1♀, {KUNHM}. Farellones, (-33.356, -70.324), 2179m, 5/i/1992, [L.Peña], 1♀, {AMNH}. Pudahuel, (-33.443, -70.772), 467m, 29/i/1951, [L.Penã], 1♂, {KUNHM}. Santiago, (-33.436, -70.636), 566m, i/1951, [Peña], 1♂, {MACN}. **Region VI:** El Peumo, (-33.972, -71.763), 192m, i/1953, [L.Peña], 1♀, {KUNHM}. La Correana, 15/ii/1977, [L.Peña], 1♀1♂, {AMNH}. **Region VII:** Constitución, (-35.335, -72.419), 51m, i/1994, [Arriagada], 1♀, {AMNH}. E of Lago Colbun, (-35.686, -71.221), 485m, 28/xii/2006, [L.Packer], 1♀, {PCYU}. Linares, (-35.847, -71.606), 158m, i/1953, [Peña], 1♂, {KUNHM}. Río Longaví, 5/xii/1967, [Catillo], 1♀, {MACN}. Río Teno, 25/i/1968, [L.Peña], 1♂, {AMNH}. **Region VIII:** Cobquecura, (-36.138, -72.794), 43m, i/1967, [P.Ramirez], 1♀, {AMNH}. Concepción, (-36.752, -73.040), 19m, 20/i/1907, [P.Herbst], 1♂, {AMNH}. Fundo El Chillán, 10/i/1981, [L.Peña], 1♀, {AMNH}. Ñuble, (-36.599, -72.072), 139m, i/1902, 1♀, {MNHP}. **Region IX:** Lago Galletué, (-38.777, -71.246), 1166m, 20/i/1962, [L.Peña], 1♂, {AMNH}.



**Figure 23.** Dorsal view of the male terminalia of *C. cyaniventris*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Range:** Chile (III–IX). See also Fig. 3A.

**Biogeographic distribution:** Andean region: Central Chilean sub-region (Coquimban and Santiaguan provinces); Subantarctic sub-region (Maule province). Central Chilean species distributed at altitudes of 0–2200m a.s.l.

**DNA barcode:** Available. BOLD: AAV8114 (1♀). Distance from the nearest neighbour (*C. nigrutilus*): 6.35–6.53%.

**Floral hosts:** Compositae – *Baccharis linearis* (Ruiz & Pav.) Pers. [Ruiz 1944 (as *B. rosmarinifolia* Hook. & Arn.)]. Escalloniaceae – *Escallonia* sp. (Toro 1999). Quillajaceae – *Quillaja saponaria* Molina (Ruiz 1944). Rhamnaceae – *Colletia spinosissima* J. F. Gmel. (this study); *C. ulicina* [Ruiz 1944 (as *C. ulcina*)].

**Comments:** Uncommon species restricted to central Chile. *Colletes cyaniventris* is the largest species of the genus found in Chile, although variation in body size (11–13.5 mm and 8.5–11 mm for females and males, respectively) is quite considerable.

In this study, the name *C. cyaniventris* is resurrected from synonymy and proposed to be the valid name for the species that has been traditionally referred to as *C. cyanescens* (see the synonymy list above), which, in turn, is here considered the senior synonym of *C. seminitidus*

(refer to “Comments” for *C. cyanescens* for further clarification). The conundrum involving these names began very early in the 20<sup>th</sup> century, when Cockerell (1904: 257) synonymized *C. cyaniventris* under *C. cyanescens*. Although this nomenclatural act has not been acknowledged by a series of authors (e.g. Vachal 1909: 54; Friese 1910: 653, 1912: 366; Toro 1986: 122; Rojas & Toro 1993: 86), many others started using the name *C. cyanescens* to refer to the large species with completely black mesosomal pubescence and metallic bright-blue metasoma (which is herein determined as *C. cyaniventris*) found in central Chile. At the same time, the comparatively smaller species with mixed black and off-white hairs on mesosoma and metallic dark-blue mesosoma (which is herein determined as *C. cyanescens*) began being identified as *C. seminitidus* (e.g. Claude-Joseph 1926: 130, Jaffuel & Pirion 1926: 364, Gazulla & Ruiz 1928: 300, Ruiz 1944: 217, Roig-Alsina 1991: 259, Toro 1999: 30, Moure & Urban 2002: 20, Packer *et al.* 2005: 197, Zayed *et al.* 2005: 1018, Montalva & Ruz 2010: 22). The nomenclatural acts proposed in this study, however, correct the mistake made by Cockerell and stabilize the use of these nominal taxa.

Even though I have not examined the lectotype of *C. cyaniventris*, the combination of the female characteristics listed in the original description by Spinola – *i. e.* pubescence black, metasoma metallic blue, smooth and nearly bare, and wing veins black (Spinola 1851: 224) – allows the determination of the species’ identity with certainty.

### ***Colletes flaminii* Moure, 1956**

(Figs. 24A–F)

*Colletes flaminii* Moure, 1956: 203; Pérez & Cerda 1980: 100; Toro 1986: 122, 1999: 27; Moure & Urban 2002: 9; Moure *et al.* 2007: 681; Montalva & Ruz 2010: 21; Ascher & Pickering 2017.

Holotype ♀ (examined). {DZUP}.





**Figure 24.** *Colletes flaminii* Moure, 1956. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

**Diagnosis:** *Colletes flaminii* is similar to *C. atripes*, *C. bicolor*, and *C. fulvipes*, however, it is unique in having the following combination of characteristics: mesepisternal interspaces imbricate (interspaces smooth in *C. bicolor*), tibiae dark-brown to black (tibiae pale-orange in *C. fulvipes*), and metasoma metallic blue (metasoma black in *C. atripes*).

**Redescription:** FEMALE (Figs. 24A, 24C, 24E):

*Dimensions (mm):* Approximate body length 9.2–9.9; head width 3.6–3.9; head length 2.6–2.8; intertegular distance 3.0–3.3; forewing length 6.8–7.2.

*Colouration:* Black except reddish-brown on distal half of tarsal claws; marked on distal half of mandible. Pale-brown on tibial spurs, medio and distitarsi, proximal half of tarsal claws, tegula, wing veins (except vein R and those enclosing marginal cell dark-brown). Dark-brown on anterior surface of trochanters and femora, dorsal surface of basitarsi, stigma, S6. Metallic dark-blue (with purple and blueish-green reflections) on metasoma (except T6 black).

*Structure:* Labrum medially convex; convexity not margined by ridges. Clypeal mid-longitudinal area evenly narrowly (0.3x MOD) and shallowly depressed on upper 3/4; adjacent lateral convex; apicomedial ridge present. Malar area 1.4x as long as basal depth of mandible (42:30). F1 1.4x as long as its apical width (42:30). UID:LID (81:73). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.35x as long as metanotum (18:50); metapostnotal pits poorly and irregularly delimited; posterior transverse carina sinuous and broadly interrupted medially. Posteromedial surface of front coxa bearing long spine (0.6x MOD). Posterior hind tibial spur ciliate. Hind basitarsus ~3x longer than broad (65:22). Inner rami of tarsal claws absent. Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Black, plumose, erect, long on lateral slopes of clypeus and supraclypeal area, interantennal, paraocular and genal areas, mesepisternum, metepisternum, mid and hind coxae, posteroventral surface of front trochanter, ventral surface of mid trochanter, T1, S1; such hairs very long on upper margin of lateral surface of propodeum, ventral surface of hind trochanter and femur; moderately short on disc of T2. Interocellar area and pronotal lobe with mixed off-white and black, plumose, erect, long hairs. Ferruginous, plumose, erect, moderately long on mesoscutum, scutellum, metanotum. Black, erect, moderately long setae on mandible, front coxa, dorsal surface of front tibia and basitarsus, dorsal surface of mid and hind tibiae and

basitarsi, T3 laterally, T4–T5, S3–S5; such hairs very long on posterior margin of mid and hind basitarsi. Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. Pale-yellow, suberect, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. S2 with pale-yellow, erect, moderately short hairs, which are branched only apically.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and moderately finely punctate; adjacent convex area longitudinally striate; lateral slopes smooth. Supraclypeal area impunctate and imbricate. Malar area substrigulate on lower 1/4; costulate elsewhere. Lower paraocular area punctures crowded. Upper paraocular and frontal areas densely and moderately finely punctate, interspaces imbricate and dull. Vertexal area finely and moderately densely punctate (interspaces smooth); coarser and denser towards lateral ocellus (interspaces rugulose). Mesoscutum, scutellum, and mesepisternum moderately finely and densely punctate (except moderately sparsely punctate on mesoscutal mid-posterior area and scutellar anterior margin); interspaces imbricate (except smooth on mesoscutal posterior 2/3 and rugulose on scutellar posterior margin). Metanotal densely and moderately finely punctate; interspaces imbricate. Metepisternum rugose above; obliquely striate medially; areolate below. Lateral surface of propodeum imbricate. Upper area of vertical surface of metapostnotum imbricate medially. Metasoma finely and densely punctate (except sparsely punctate on S6); interspaces smooth (except imbricate on metasomal imbricate).

MALE (Figs. 24B, 24D, 24F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 7.8–8.3; head width 3.0–3.2; head length 2.5–2.6; intertegular distance 2.1–2.4; forewing length 6.2–6.6.

*Colouration:* Mandibular reddish-brown area restricted to distal 1/3. Dorsal surface of tibiae dark-brown. Metasomal terga without green reflections.

*Structure:* Clypeal mid-longitudinal area evenly narrowly (0.3x MOD) and shallowly depressed. Malar area ~1.6x as long as basal depth of mandible (52:32). F1 slightly longer than its apical width (46:44). UID:LID (54:44). Dorsolateral angle of pronotum rounded. Horizontal surface of metapostnotum ~0.55x as long as metanotum (26:46). Posteromedial surface of front coxa without spine. Hind basitarsus ~4x longer than broad (67:17). Outer rami of hind tarsal

claw 2x as long as inner rami (22:16). S7, S8 and genital capsule as in Figs. 25A, 25B, 25C, respectively.

*Pubescence*: Off-white except bright-yellow on axilla, scutellum, metanotum; paraocular area with a longitudinal band of black hairs; T4–T7 with fulvous setae. Plumose on front coxa.

*Surface sculpture*: Clypeal striae restricted to lower 1/5. Supraclypeal area with sparse shallow punctures; interspaces rugulose. Paraocular area moderately densely punctate below. Lateral surface of propodeum areolate.

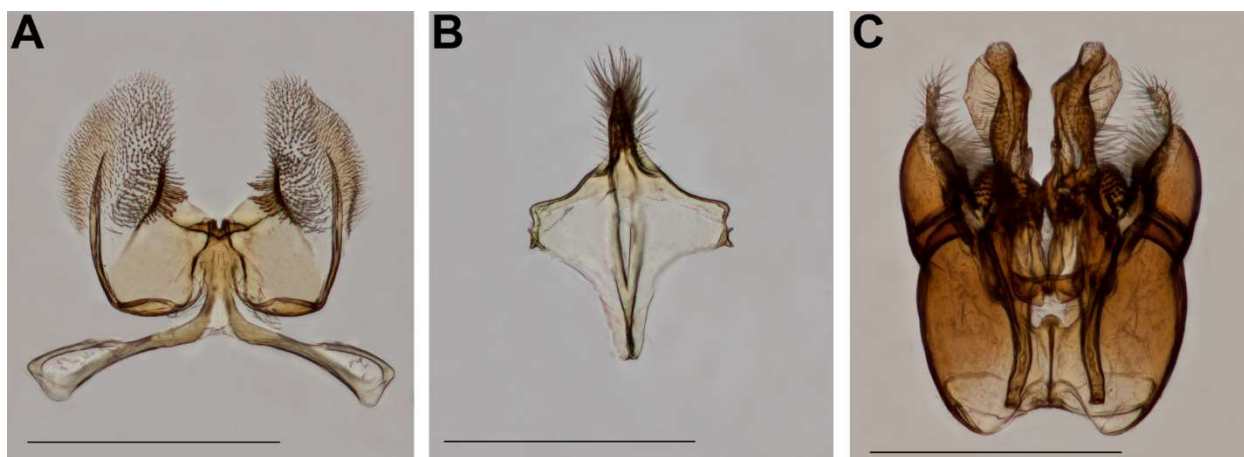
**Material studied:** *Primary type specimen*: Holotype ♀ – “HOLOTYPUS”. “flaminii; Det. J. S. Moure 56”. “TEMUCO; xi-1929; Constitución; Prof. MONTERO”. {DZUP}.

*Additional specimens*: **ARGENTINA – Río Negro**: Bariloche, (-41.138, -71.274), 824m, xii/1964, [A.Giai], 1♂, {MACN}. Río Pichi Leufu, xi/1964, [A.Giai], 1♀, {MACN}. **Chubut**: Esquel, (-42.894, -71.135), 789m, 20/xii/2006, [L.Packer], 1♀, {PCYU}; idem, except 2/i/1951, [J.Foerster], 1♀, {DZUP}. **Santa Cruz**: 25km E of Los Antiguos, (-46.621, -71.308), 255m, 1/iii/2007, [Gravel & Gravel], 9♀♀, {PCYU}; idem, except 24/xii/2006, [L.Packer], 1♀.

**CHILE – Region VII**: W of Laguna del Maule, (-35.997, -70.560), 2156m, 3/i/2009, [L.Packer], 2♀♀, {PCYU}. El Planchón, (-34.149, -70.530), 1149m, 1/ii/2003, [A.Ugarte], 1♀, {PCYU}. **Region VIII**: Termas de Chillán, (-36.909, -71.418), 1561m, 14/i/1993, [H.Toro], 1♂, {AMNH}; idem, except 19/i/1979, [L.Peña], 1♀. **Region IX**: Río Liucura, 9/xii/2004, [Ascher & Kawahara], 1♂, {AMNH}. **Region XI**: Chile Chico, (-46.550, -71.716), 218m, 16/i/1956, [G.Kuschel], 1♀, {KUNHM}; idem, except 14/ii/1982, [B.Dyer], 1♂, {DZUP}. **Region XII**: 4km W of Laguna Amarga, (-50.965, -72.819), 159m, 7/xii/1966, [E.Schlinder], 1♂, {AMNH}. Brazo Norte, (-52.237, -70.412), 173m i/1972, [M.Cerda], 1♀, {AMNH}. Laguna Azul, (-50.875, -72.726), 225m, xii/1978, [W.Sielfeld], 1♀, {AMNH}; idem, except 1♀, {DZUP}.

**Range**: Argentina (Río Negro, Chubut, Santa Cruz), Chile (Regions VII–XII). See also Fig. 19C.

**Biogeographic distribution**: Andean region: Central Chilean sub-region (Santiaguan province); Subantarctic sub-region (Magellanic Forest province); Patagonian sub-region (Patagonian province). Central Chilean and southwestern Argentinean species distributed at altitudes of 100–2200m a.s.l.



**Figure 25.** Dorsal view of the male terminalia of *C. flaminii*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**DNA barcode:** Available. BOLD: AAO3445 (2♀♀1♂). Barcoded specimens from Chile and Argentina were assigned the same BIN (see Table S1). Distance from the nearest neighbours: 2.8–3.13% (*C. fulvipes*) and 6.1–6.12% (*C. chusmiza*).

**Floral hosts:** Compositae – *Taraxacum campylodes* G. E. Haglund [Pérez & Cerda 1980 (as *T. officinale* (L.) Weber ex F. H. Wigg.)]. Lamiaceae – *Nepeta racemosa* Lam. [Pérez & Cerda 1980 (as *N. mussinii* Spreng. ex Henckel)]. Leguminosae – *Adesmia* sp. (this study); *Trifolium* sp. (Pérez & Cerda 1980).

**Comments:** Uncommon species with a broad geographic range in southern South America. As far as the data suggest, its activity period spans from November to February.

Moure's description of *C. flaminii* was based on a single female with weakly pigmented pubescence and integument, which, according to Toro (1999), was probably a recently emerged specimen from the nest. The male was only described several decades later (Toro 1999: 28). This species was not included by Rojas & Toro (1993) in their key for the Chilean species with metallic blue metasoma.

***Colletes flavipilosus* Ferrari, new species**

(Figs. 26A–F)

**Diagnosis:** *Colletes flavipilosus* **n. sp.** can be readily diagnosed through the combination of body pubescence pale-yellow, mesepisternal interspaces imbricate, T1–T5 covered with appressed hairs (except T1 in males), and marginal zones of metasomal terga pale-yellow, contrasting with the black discs.

*Colletes flavipilosus* **n. sp.** is most similar to *C. patagonicus*, but these species can be easily differentiated from each other by the overall pale-yellow mesosomal pubescence in the former (in *C. patagonicus*, the scutellar and metanotal pubescence is ferruginous, which strongly contrasts with the partially (females) to entirely (males) pale-yellow mesoscutal pubescence); and by T2–T5 covered with appressed hairs in *C. flavipilosus* **n. sp.** (T2–T5 with erect hairs only, in *C. patagonicus*).

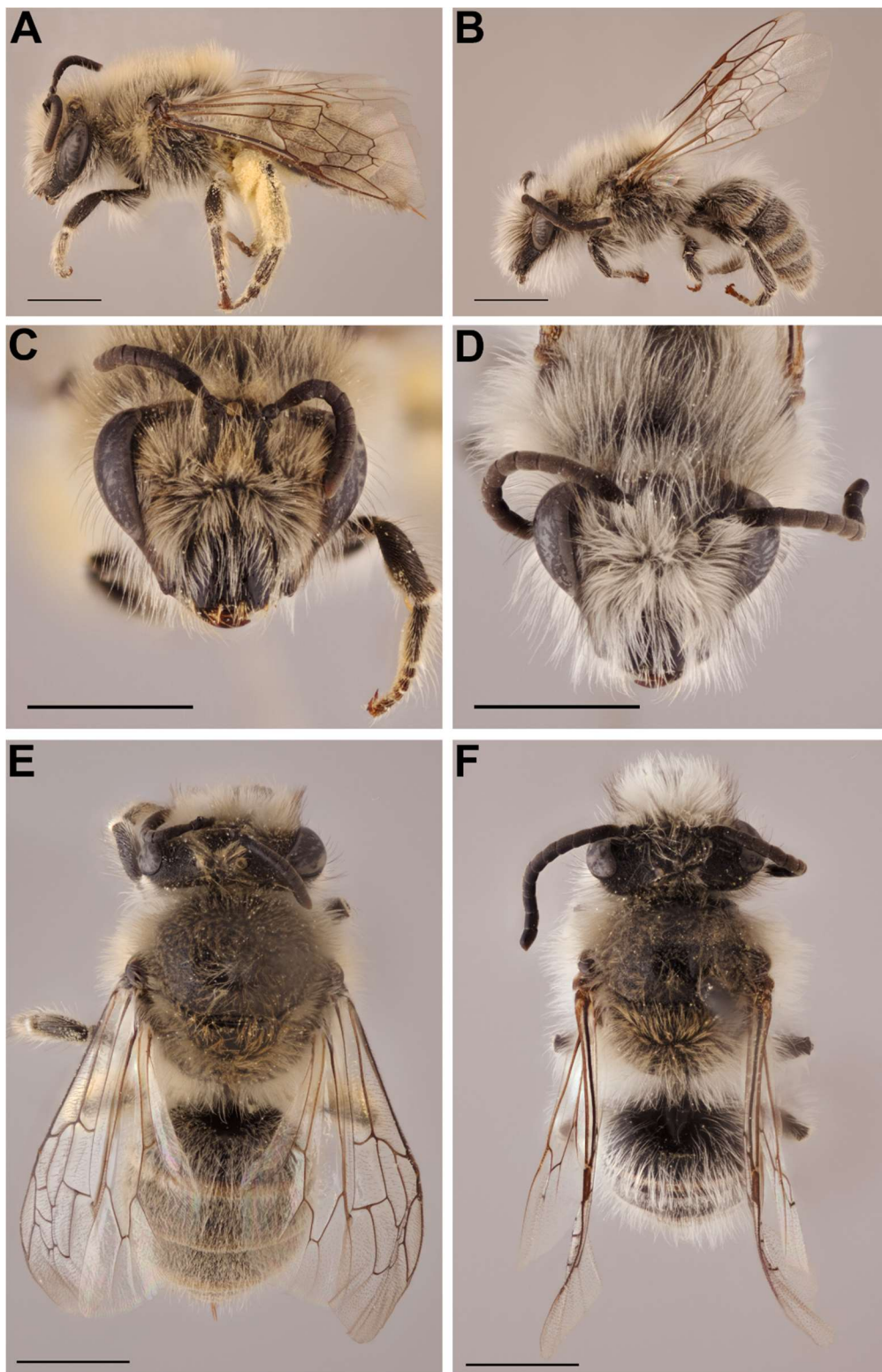
**Description:** FEMALE (Figs. 26A, 26C, 26E):

*Dimensions (mm):* Approximate body length 7.2; head width 2.8; head length 2.2; intertegular distance 2.2; forewing length 6.1.

*Colouration:* Black except dark-brown on wing veins (except vein R of forewing black), distitarsi (except distal 1/4 pale-brown). Pale-yellow on tibial spurs, marginal zones of T1–T5 and S1–S5. Pale-brown on proximal half of tarsal-claws, ventrally reflexed lateral areas of T1, mid-longitudinal band of S6. Reddish-brown on distal half tarsal claws; marked on distal half of mandible.

*Structure:* Labrum medially convex; convexity not margined by ridges. Clypeal mid-longitudinal area evenly shallowly and narrowly (0.4x MOD) depressed on upper 4/5; adjacent lateral area convex; apicomedial ridge absent. Malar area ~1.4x as long as basal depth of mandible (43:30). F1 ~1.3x as long as its apical width (28:22). UID:LID (61:58). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded dorsolaterally. Horizontal surface of metapostnotum ~0.5x as long as metanotum (17:35); metapostnotal pits well-delimited; posterior transverse carina sinuous and interrupted medially. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate.





**Figure 26.** *Colletes flavipilosus* Ferrar, n. sp. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

Hind basitarsus ~3.8x longer than broad (49:13). Outer rami of hind tarsal claws ~2x as long as inner rami (22:12). Posterolateral area of S6 convex but without ridge; marginal zone depressed.

*Pubescence:* Pale-yellow throughout (except paraocular area with pale-yellow and black hairs intermingled). Plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, pronotal lobe, ventral surface of mid trochanter, ventral margin of mid femur, mid and hind coxae, S1; such hairs long on interantennal, frontal and genal (except very long near proboscidal fossa) areas, mesoscutum, scutellum, metepisternum, anteroventral surface of front trochanter and femur, ventral surface of hind trochanter; very long on vertexal area, metanotum, mesepisternum, upper margin of lateral surface of propodeum. Erect, moderately short setae on dorsal surface of hind tibia and basitarsi; moderately long on mandible, ventral surface of front coxa, posterior margin of basitarsi (except very long on hind basitarsus). Suberect, short setae on dorsal surface of front and mid tibiae; thicker setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T1–T5 covered with dense appressed hairs (except slightly sparser on T1); T1–T3 also with plumose, erect, moderately long hairs (except long on T1); T4–T5 also with erect, moderately long setae (T5 with pale-yellow and black hairs intermixed). S2 with erect, short hairs, which are branched only apically. Discs of S3–S5 covered with suberect, short setae; erect, longer on marginal zone; marginal zones of S3–S4 also with a line of plumose hairs. S6 largely bare.

*Surface sculpture:* Clypeal mid-longitudinal depression moderately finely and moderately densely punctate; adjacent convex area with very sparse punctures; interspaces smooth and shiny throughout. Malar area sparsely and moderately finely punctate on upper half; interspaces imbricate. Supraclypeal area with very sparse, moderately fine punctures near lateral slopes; interspaces imbricate. Paraocular area punctures crowded and moderately coarse below; moderately fine and moderately dense above. Frontal area moderately finely and moderately sparsely punctate; interspaces rugulose and dull. Vertexal area finely and densely punctate; interspaces rugulose (except rugose near ocellus and eye). Mesoscutum moderately finely and moderately densely punctate (except sparsely punctate on mid-posterior area); interspaces smooth and shiny. Scutellum sparsely and moderately finely punctate (except finely and densely near posterior margin); interspaces imbricate. On metanotum, punctures limits very difficult to discern from the rugulose interspaces. Mesepisternum moderately sparsely and moderately finely

(except densely punctate near scrobe); interspaces imbricate. Metepisternum rugose above; obliquely striate medially; rugulose below. Lateral surface of propodeum rugose. Upper margin of vertical surface of metapostnotum imbricate medially. Metasomal terga minutely and sparsely punctate; interspaces smooth. S2–S5 finely and densely punctate laterally; sparsely punctate mid-longitudinally; interspaces imbricate. S6 sparsely and moderately finely punctate.

MALE (Figs. 26B, 26D, 26F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 6.9; head width 2.7; head length 2.1; intertegular distance 2.2; forewing length 6.0.

*Colouration*: Mandibular reddish-brown spot restricted to distal 1/3. Tegula dark-brown. Wing veins pale-brown. Marginal zones of T6 and S6 pale-yellow.

*Structure*: Clypeal mid-longitudinal area evenly shallowly and broadly (0.7x MOD) depressed. Malar area ~1.4x as long as basal depth of mandible (49:24). F1 ~1.2x as long as its apical width (30:24). UID:LID (61:53). Genal area concave behind upper summit of compound eyes in lateral view. Horizontal surface of metapostnotum 0.4x as long as metanotum (16:40); metapostnotal pits poorly-delimited. Hind basitarsus ~3x longer than broad (45:12). Outer rami of hind tarsal claws 1.8x as long as inner rami (18:10). Posterolateral area of S6 convex but without ridge; marginal zone depressed. S7, S8 and genital capsule as in Figs. 27A, 27B, 27C, respectively.

*Pubescence*: Genal area with a line of black hairs near eye. Disc of T1 not covered with appressed hairs; on T2–T5, appressed hairs much sparser (integument not obscured). Marginal zone of S3 with setae only. S6 covered with erect, short setae.

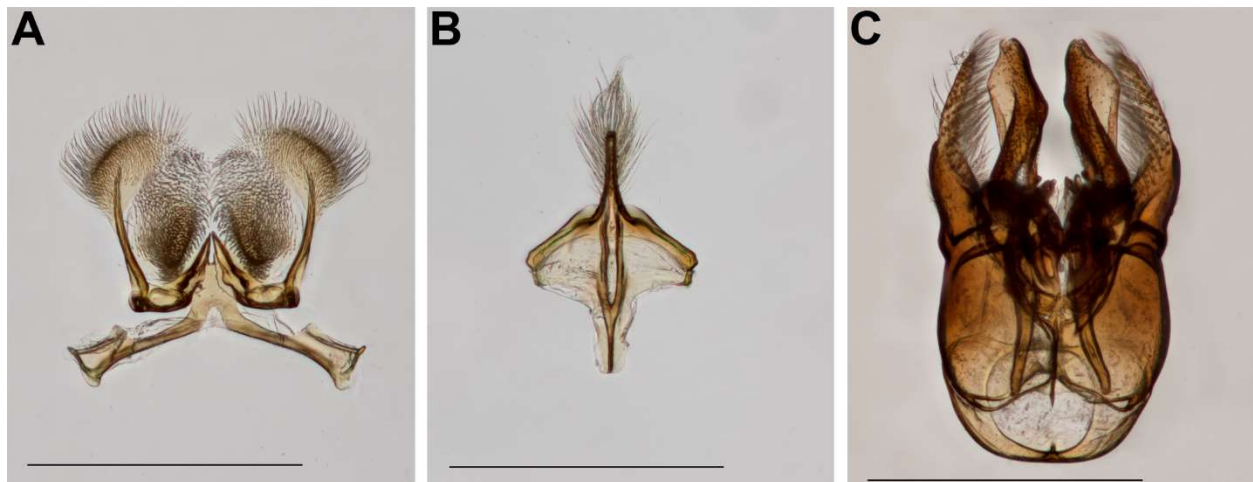
*Surface sculpture*: Mid-longitudinal depression densely punctate. Vertexal area punctures crowded. Mesoscutal interspaces imbricate. Scutellum densely punctate. Upper area of vertical surface of propodeum rugose. Metasomal tergal imbrication restricted to marginal zones; punctation dense and moderately fine (except sparse on T1 mid-longitudinally); T1 with rugulose interspaces. S6 densely punctate laterally.

**Type material:** *Holotype* ♀ – “CHILE Region VII; Laguna del Teno, 2548m; -35.10666 - 70.53926; 26.i.2016, L. Packer”. “CCDB-28313 F09”. “HOLOTYPE; *Colletes flavipilosus* ♀; Ferrari, new species”. {PCYU}.

**Paratypes:** **CHILE – Region V:** Portillo, (-32.837, -70.129), 2874m, 30/xii/2008, [L.Packer], 1♂, {PCYU}. **Region Metropolitana:** Valle Nevado, (-33.362, -70.257), 2667m, 31/xii/2008, [L.Packer], 1♂, {PCYU}. **Region VII:** El Planchón, (-34.149, -70.530), 1149m, 1/ii/2003, [A.Ugarte], 1♂, {PCYU}. Laguna del Maule, (-36.020, -70.499), 2352m, 5/i/2009, [L.Packer], 1♀7♂♂, {PCYU}; idem, except 29/xii/2006, [Packer & Gravel], 1♂. Portillo, (-32.851, -70.134), 2608m, 30/xii/2008, [L.Packer], 1♂, {PCYU}. W of Laguna del Maule, (-35.999, -70.426), 2384m, [L.Packer], 1♂, {PCYU}. **Region IX:** Questa las Raices, (-38.429, -71.448), 1591m, 4/i/2013, [L.Packer], 1♂, {PCYU}.

**Range:** Chile (Regions V–IX). See also Fig. 10C.

**Biogeographic distribution:** Andean region: Central Chilean sub-region (Coquimban and Santiaguan provinces); Subantarctic sub-region (Maule province). Central Chilean species distributed at altitudes of 1100–2900m a.s.l.



**Figure 27.** Dorsal view of the male terminalia of *C. flavipilosus* n. sp. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**DNA barcode:** Available. BOLD: ACV1795 (1♀), BOLD: AAO3408 (1♀3♂♂). Specimens with different BINs were caught in the same locality on the same date (see Table S1). Distance between BINs: 0.64–2.41%. Distance from the nearest neighbour (*C. patagonicus*): 3.22–3.82%.

**Floral hosts:** Boraginaceae – *Phacelia* sp. Loasaceae – *Loasa filicifolia* Poepp.

**Etymology:** Refers to the fact that the species is entirely covered with pale-yellow pubescence.

**Comments:** *Colletes flavipilosus* **n. sp.** is remarkably similar to *C. patagonicus* in terms of structure (including male terminalia) and surface sculpture. However, *C. flavipilosus* **n. sp.** and *C. patagonicus* can be easily distinguished from one another by their unique patterns of mesosomal and metasomal pubescence (refer to “Diagnosis”, above). Moreover, these species have not been found occurring sympatrically, nor even parapatrically: *C. flavipilosus* **n. sp.** ranges from Regions V to IX (southernmost latitude: -38.429), whereas *C. patagonicus* is found in the far south of South America, ranging from the Chilean Regions X (northernmost latitude: -40.754) to XII and from the Argentinean provinces of Río Negro, Chubut and Santa Cruz. Besides, females of these species seem to visit different plant families: *C. flavipilosus* **n. sp.** has been found foraging on flowers of *Phacelia* Juss. (Boraginaceae) and *Loasa* Adans. (Loasaceae), while *C. patagonicus* visits *Nepeta* (Lamiaceae) and *Trifolium* (Leguminosae). Therefore, recognition of two distinct species is supported by morphological, geographic and floral evidence.

### ***Colletes fulvipes* Spinola, 1851**

(Figs. 28A–F)

*Colletes fulvipes* Spinola, 1851: 225; Ruiz & Stuardo 1935: 322; Toro 1986: 122, 1999: 27; Rojas & Toro 1993: 86; Moure & Urban 2002: 9; Moure *et al.* 2007: 681; Montalva & Ruz 2010: 21; Ascher & Pickering 2017.

Lectotype ♂ (examined) designated by Moure & Urban (2002: 9). {MNHP}.

*Colletes fulpis* (sic); Dalla Torre 1896: 41.

*Colletes flavipes* (sic); Ruiz 1935: 271.





**Figure 28.** *Colletes fulvipes* Spinola, 1851. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.



**Diagnosis:** The combination of pale-orange tibiae and tarsi, and metallic blue mesosoma differentiates *C. fulvipes* from all *Colletes* species found in Chile, except *C. quehu*. However, these species can be readily distinguished by the following combination of female features (as the male *C. quehu* is still unknown): body length about 12mm in *C. fulvipes* (*C. quehu* is about 9mm long); facial and mesosomal pubescence ferruginous in *C. fulvipes* (pale-yellow in *C. quehu*); and clypeal mid-longitudinal carina very short in *C. fulvipes*, restricted to the lower 1/4 of clypeus (clypeal carina very long in *C. quehu*, extending almost throughout, absent for upper 1/5 only).

**Redescription:** FEMALE (Figs. 28A, 28C, 28E):

*Dimensions (mm):* Approximate body length 11.2–12.1; head width 3.5–3.9; head length 2.6–2.9; intertegular distance 3.3–3.7; forewing length 7.4–8.0.

*Colouration:* Black except pale-orange on distal ring of front and mid femora, tibiae, tarsi, distal half of hind femur, proximal half of tarsal claws, stigma, wing veins enclosing marginal cell. Reddish-brown on distal half of tarsal claws; marked on distal 1/3 of mandible. Dark-orange on apical ring of pedicel and flagellum ventrally. Pale-orange on tibial spurs, tegula, wing veins (except those enclosing marginal cell). Metallic-blue on T1–T5 (with purple and blueish-green reflections on discs). Metallic dark-blue on mesoscutal disc, metasomal sterna.

*Structure:* Labrum medially convex; convexity not margined by ridges. Clypeal mid-longitudinal area neither depressed nor carinate; adjacent lateral area convex; apicomedial ridge present. Malar area subequal to basal depth of mandible (34:32). F1 ~1.5x as long as its apical width (56:38). UID:LID (83:76). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.4x as long as metanotum (26:62); propodeal pits well-delimited; posterior transverse carina sinuous and narrowly interrupted medially. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus 3.2x longer than broad (58:18). Outer rami of hind tarsal claws 4x as long as inner rami (32:8). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Ferruginous, plumose, erect, long on lateral slopes of supraclypeal area, interantennal, upper paraocular, frontal and vertexal (behind lateral ocellus) areas, pronotal lobe, mesoscutum, scutellum; such hairs very long on metanotum, upper margin of lateral surface of

propodeum. Black, plumose, erect, long on lower paraocular area, upper genal area, lateral surface of propodeum, T1; such hairs very long on lower genal area, mesepisternum, metepisternum, ventral surface of front and mid coxae, trochanters. Pale-yellow, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. Fulvous, erect, moderately long setae on mandible, clypeal mid-longitudinal area, posterior surface of front coxa, ventral surface of front trochanter, dorsal surface of mid tibia. Ferruginous, suberect, moderately long setae on dorsal surface of mid and hind basitarsi and hind tibia; such hairs erect, very long on posterior margin of mid and hind basitarsi. Pale-orange, moderately short, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Black, erect, moderately short setae on T2–T5 (except longer on T4–T5 laterally), S2–S6.

*Surface sculpture:* Clypeal mid-longitudinal area densely and moderately finely punctate; lower 1/5 longitudinally striate. Supraclypeal area impunctate and imbricate (except smooth upper 1/5). Malar area substrigulate on lower 1/5; costulate elsewhere. Vertexal interspaces rugulose but somewhat shiny. Mesoscutum moderately coarsely punctate; very densely punctate on anterior and lateral areas; moderately sparsely punctate on disc and posterior margin; interspaces smooth and shiny throughout. Scutellum moderately coarsely and densely punctate on disc; denser and finer on posterior margin. Metanotal punctation difficult to discern from the dull rugulose interspaces. Mesepisternum evenly densely and moderately coarsely punctate; interspaces imbricate. Metepisternum obliquely striate medially; rugulose above and below. Lateral surface of propodeum sparsely and finely punctate; interspaces imbricate. Vertical surface of metapostnotum rugulose medially. Metasomal terga very finely punctate; moderately dense on T1; dense on T2–T5; interspaces smooth throughout.

MALE (Figs. 28B, 28D, 28F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.6–9.2; head width 3.1–3.4; head length 2.2–2.4; intertegular distance 2.2–2.5; forewing length 6.6–7.0.

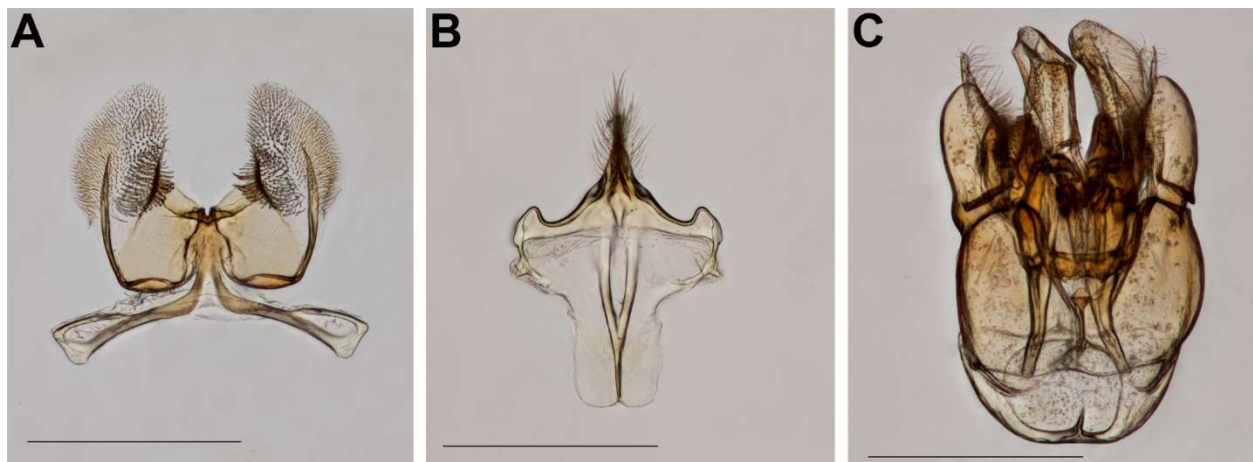
*Colouration:* Mid 2/4 of dorsal surface of front tibia dark-brown. Stigma, wing veins enclosing marginal cell pale-orange. Ventral surface of antenna, mid 1/3 of hind femur black.

*Structure:* Clypeal lower mid-longitudinal area slightly swollen but lacking ridges. Malar area 1.75x as long as basal depth of mandible (42:24). F1 ~1.3x as long as its apical width

(38:30). UID:LID (88:76). Genal area concave behind upper summit of compound eyes in lateral view. Horizontal surface of metapostnotum  $\sim 0.4\times$  as long as metanotum (26:64). Hind basitarsus  $\sim 3.2\times$  longer than broad (55:17). Outer rami of hind tarsal claws  $\sim 1.7\times$  as long as inner rami (20:12). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 29A, 29B, 29C, respectively.

*Pubescence*: Ferruginous on mesepisternum, metepisternum, lateral surface of propodeum, T1 ferruginous. Pale-yellow on face (except paraocular area), genal area (near proboscidal fossa), trochanters, anterior surface of front femur and tibia, ventral margin of mid femur. Fulvous, plumose, moderately long on T2.

*Surface sculpture*: Clypeal mid-longitudinal depression punctures crowded. Supraclypeal area with very sparse moderately coarse punctures. Mesoscutal mid-posterior area sparsely punctate. Mesepisternum densely punctate. T1 interspaces rugulose.



**Figure 29.** Dorsal view of the male terminalia of *C. fulvipes*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** *Primary type specimen*: Lectotype ♂ – “MUSEUM PARIS; CHILI; GAY 15-43”. “♂”. “288”. “TYPE”. “Colletes; fulvipes; ♀ Spin”. “LECTOTYPE; Colletes fulvipes ♂; Spinola, 1851; labelled R. Ferrari, 2017”. {MNHP}.

*Additional specimens*: **ARGENTINA – Río Negro**: El Bolsón, (-41.965, -71.544), 315m, x/1943, [A.Prosen], 1♂, {KUNHM}. **CHILE – Region Metropolitana**: E of El Volcan, (-

33.828, -70.043), 1969m, 31/xii/2012, [Packer & Smith], 1♀, {PCYU}. Farellones, (-33.340, -70.291), 2700m, 2/i/1985, [L.Peña], 1♂, {AMNH}; idem, except 21/xii/1988, 1♀. Highway G-455 km 18.1, (-33.694, -70.112), 2333m, 26/ii/2013, [Postlethwaite & Monckton], 1♀, {PCYU}. Río Blanco, 15/xi/1969, [H.Toro], 1♀, {PUCV}. SE of San José de Maipo, 1900m, 4/ii/1984, [L.Peña], 1♀, {AMNH}. **Region VI:** La Correana, 1400m, 16/ii/1977, [L.Peña], 1♀, {AMNH}. Las Cabras, 1400m, [L.Peña], 2♀♀1♂, {KUNHM}. **Region VII:** El Planchón, (-34.149, -70.530), 1149m, 1/ii/2003, [A.Ugarte], 1♀, {PCYU}. Laguna del Maule, (-36.020, -70.499), 2353m, 5/i/2009, [L.Packer], 2♀♀, {PCYU}. **Region VIII:** Las Trancas, (-36.913, -71.500), 1225m, 14/xii/1993, [Wood & Wood], 1♀, {CNC}. Shangri-la, 1650m, 19/i/1979, [L.Peña], 2♀♀1♂, {AMNH}. Termas de Chillán, (-36.909, -71.418), 1561m, 14/i/1993, 1♂, {PUCV}; idem, except 11/xii/2006, [L.Packer], 1♀. **Region IX:** Cordillera de las Raices, (-38.523, -71.506), 1100m, 19/xii/1976, [L.Peña], 2♀♀, {AMNH}; idem, except 13/ii/1980, 1♂. Passo de Pino Hachado, 1800m, [L.Peña], 1♀, {AMNH}. Questa las Raices, (-38.436, -71.507), 1260m, 4/i/2013, [Packer & Smith], 1♂, {PCYU}.

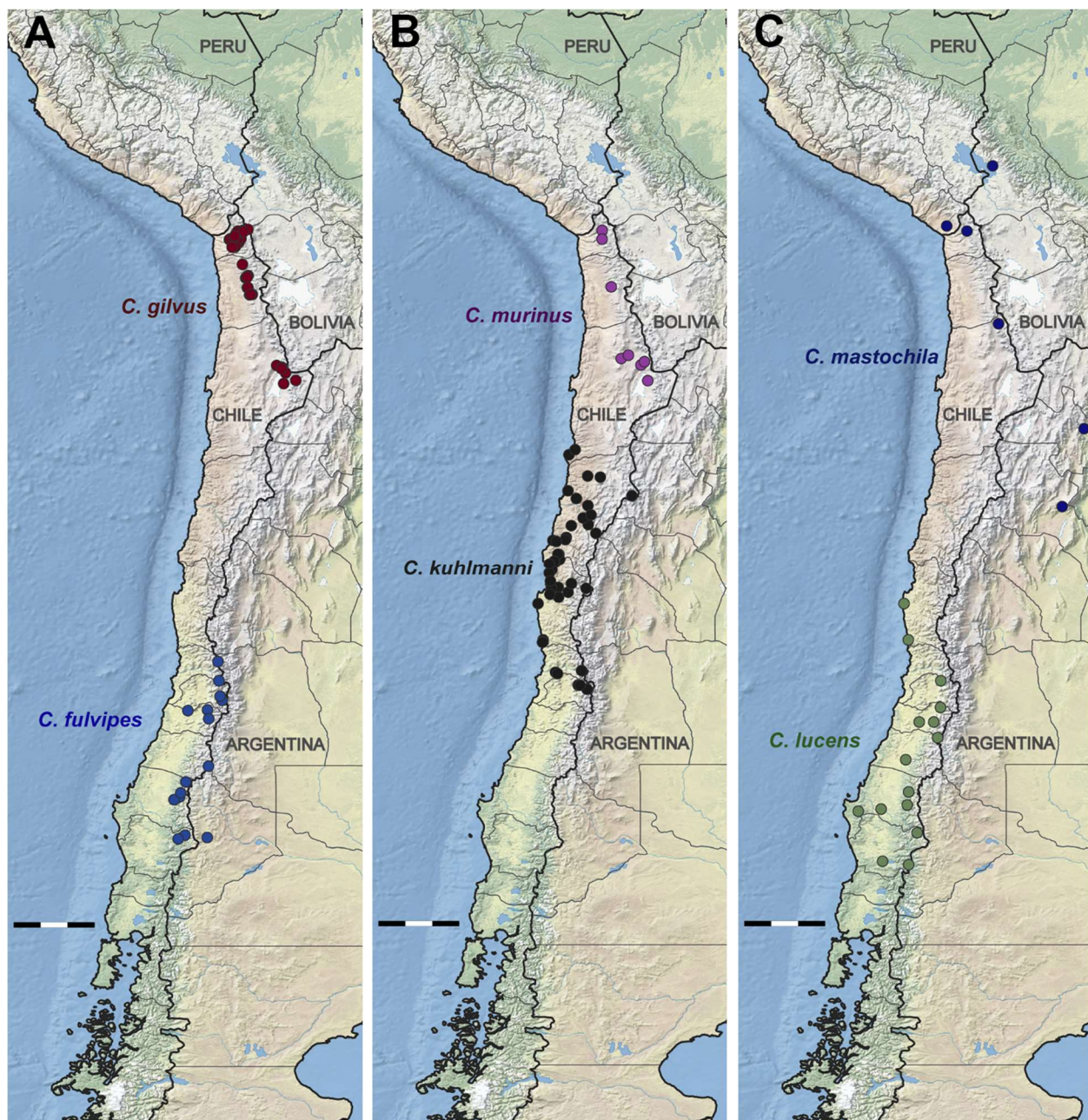
**Range:** Argentina (Río Negro), Chile (Regions Metropolitana–IX). See also Fig. 30A.

**Biogeographic distribution:** Andean region: Central Chilean sub-region (Coquimban and Santiaguan provinces); Subantarctic sub-region (Maule province); Patagonian sub-region (Patagonian province). Central Chilean and western Argentinean species distributed at altitudes of 300–2700m a.s.l.

**DNA barcode:** Available. BOLD: AAO3473 (3♀♀1♂). Distance from the nearest neighbours: 2.8–3.13% (*C. flaminii*) and 3.53–3.69% (*C. chusmiza*).

**Floral hosts:** Leguminosae – *Adesmia emarginata* Clos (Ruiz 1944).

**Comments:** Uncommon species distributed in central Chile, but also found in Argentina. Toro (1999) recorded *C. fulvipes* as far south as Aisén (Region XI), however this could not be verified.



**Figure 30.** Geographic distribution by *Colletes* species. (A) *C. gilvus* and *C. fulvipes*; (B) *C. murinus* and *C. kuhlmanni* **n. sp.**; (C) *C. mastochila* and *C. lucens*. Scale bars approximately 300 km.

Unlike all the other type specimens of the Chilean *Colletes* species described by Spinola – which are deposited at the MRSN – the lectotype of *C. fulvipes* is currently deposited at the MNHP. Unfortunately, this specimen’s head is much damaged likely due to attack by dermestid



beetles; however, the most important diagnostic characters for the species (*i.e.* the legs and metasoma) are in good condition. As noted in the “Material studied” section (see above), Spinola identified the specimen as a female, although an apparently older label correctly indicates that it is a male. The female *C. fulvipes* is here described for the first time, as only the male was known to Spinola at the time the species was described.

***Colletes gilvus* Vachal, 1909**

(Figs. 31A–F)

*Colletes gilvus* Vachal, 1909: 56; Toro 1986: 122, 1999: 28; Moure & Urban 2002: 10; Moure *et al.* 2007: 682; Almeida & Danforth 2009: 293; Kuhlmann *et al.* 2009: 296; Montalva & Ruz 2010: 22; Almeida *et al.* 2011: 7; Ascher & Pickering 2017.

Lectotype ♀ (examined). {MNHP}. [hereby designated]

*Colletes tomentosus* Friese, 1910: 648; 1912: 367; Ruiz 1944: 218; Moure & Urban 2002: 21; Moure *et al.* 2007: 688. Synonymy proposed by Toro (1999: 28).

Lectotype ♀ (examined) designated by Moure & Urban (2002: 21). {ZMB}.

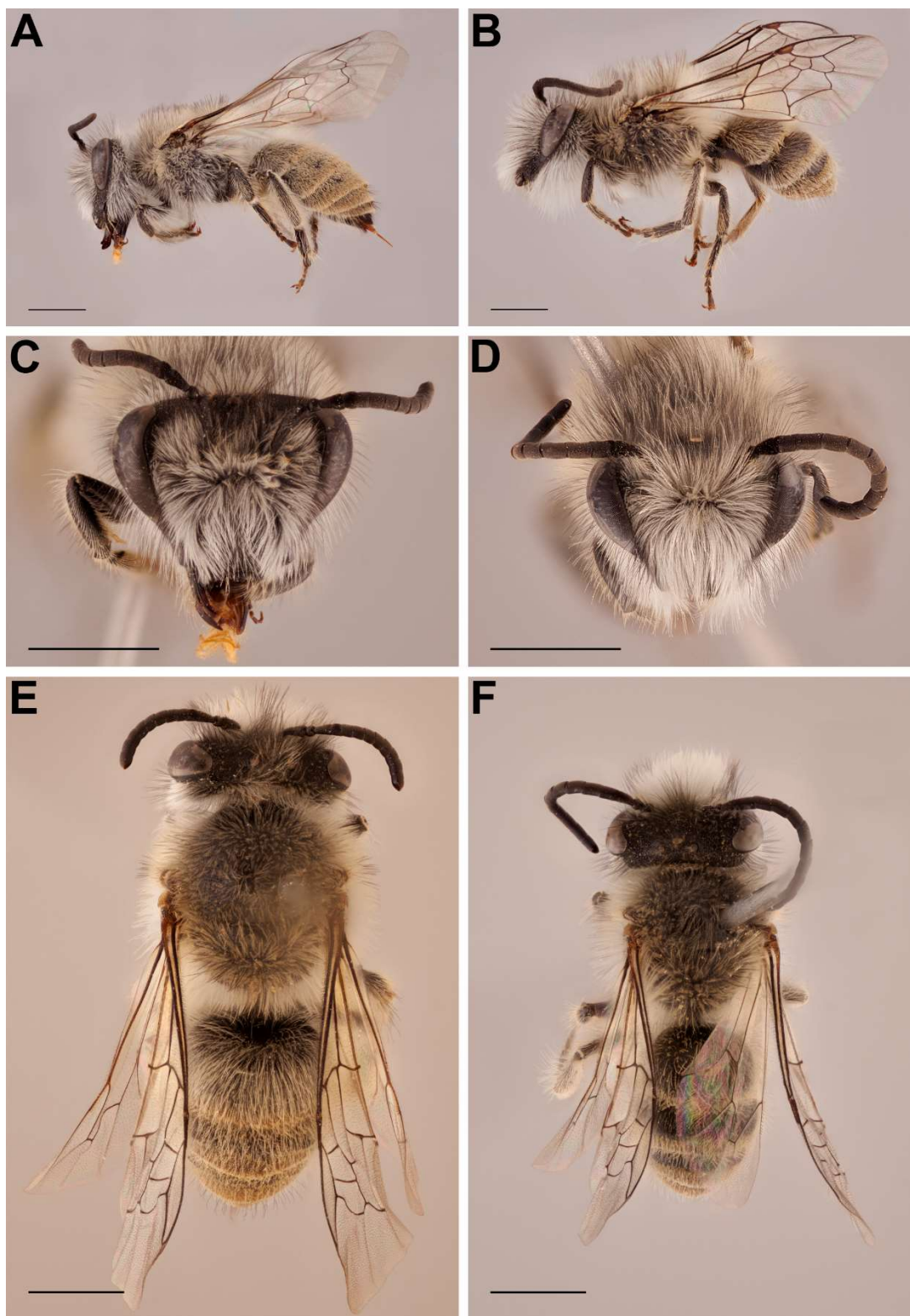
**Diagnosis:** *Colletes gilvus* can be diagnosed through the following combination of characteristics: clypeal mid-longitudinal area depressed and lacking carina, mesoscutal pubescence with pale-yellow and black hairs intermingled, malar area ~1.5x as long as basal depth of mandible, F1 at least as long as F2, and posterior hind tibial spur ciliate.

*Colletes gilvus* is most similar to *C. kuhlmanni* **n. sp.**, but these species can be differentiated by T1 moderately densely and finely punctate in *C. gilvus* (T1 sparsely and minutely punctate in *C. kuhlmanni* **n. sp.**). Besides, F1 is ~1.3x as long as its apical width in the male *C. gilvus* (F1 slightly shorter than its apical width in *C. kuhlmanni* **n. sp.**). Also, the females are distinct from one another by the disc of T1 covered with both long erect hairs and sparse appressed hairs in *C. gilvus* (T1 with only erect, long hairs in the female *C. kuhlmanni* **n. sp.**).

**Redescription:** FEMALE (Figs. 31A, 31C, 31E):

*Dimensions (mm):* Approximate body length 9.3–10.3; head width 3.1–3.4; head length 2.4–2.6; intertegular distance 2.3–2.5; forewing length 6.9–7.3.





**Figure 31.** *Colletes gilvus* Vachal, 1909. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

*Colouration:* Black except dark-brown on tegula, wing veins (except vein R of forewing black), distal 1/5 of distitarsi. Reddish-brown on distal half of tarsal claws; marked on distal 1/3 of mandible. Pale-brown on stigma, tibial spurs, proximal half of tarsal claws, marginal zones of T1–T5 and S1–S5.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area evenly deeply depressed; depression narrow (0.5x MOD) for upper 1/3, broader (1.2x MOD) on lower 2/3; adjacent lateral area convex; apicomedial ridge absent. Malar area ~1.6x as long as basal depth of mandible (47:30). F1 ~1.4x as long as its apical width (30:21). UID:LID (68:64). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum ~0.4x as long as metanotum (21:46); metapostnotal pits well-delimited; posterior transverse carina straight and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.5x longer than broad (55:16). Outer rami of hind tarsal claws 1.7x as long as inner rami (17:10). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Off-white, plumose, erect, moderately long on lateral slopes of clypeus, ventral surface of coxae (except short on hind coxa), ventral margin of mid femur, S1; such hairs long on posteroventral surface of front trochanter and femur, ventral surface of mid and hind trochanters, mesepisternum, metepisternum, T1; very long on upper margin of lateral surface of propodeum; intermingled with black hairs on paraocular, interantennal, frontal, vertexal and genal areas, pronotal lobe, mesoscutum, scutellum, metanotum. Pale-yellow, erect, moderately long setae on mandible, posterior surface of front tibia and basitarsus, dorsal surface of mid and hind tibiae and basitarsi; such hairs very long on posterior margin of mid and hind basitarsi. Pale-orange, suberect, thicker setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T1–T5 covered with pale-yellow appressed hairs; T2–T3 also with plumose, erect, moderately short hairs; T4–T5 also with black, erect, moderately long setae. S2 with pale-yellow, erect, short hairs, which are branched only apically. S3–S6 with pale-yellow, erect, short setae.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and moderately finely punctate; adjacent convex area impunctate and smooth; lower 1/3 longitudinally striate. Malar

area longitudinally striate. Supraclypeal area smooth and shiny. Paraocular area moderately punctures crowded and coarse below; sparser above. Frontal area densely and moderately coarsely punctate below (interspaces smooth); rugulose near mid ocellus. Vertexal area punctures crowded and moderately fine (except fine and dense near eye). Mesoscutum, scutellum and mesepisternum densely and moderately coarsely punctate (except mesoscutal mid-posterior area sparsely punctate and scutellar posterior 1/5 punctures crowded); interspaces smooth and shiny. Metanotum punctures crowded and moderately fine. Metepisternum rugulose above; obliquely striate medially; smooth below. Lateral surface of propodeum sparsely and moderately finely punctate; interspaces smooth. Upper area vertical surface of metapostnotum smooth medially. T1 moderately densely punctate; fine punctures intermingled with moderately fine ones. T2–T5 densely and finely punctate. Metasomal terga interspaces smooth throughout. S1–S6 sparsely and moderately coarsely punctate; interspaces imbricate.

MALE (Figs. 31B, 31D, 31F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 7.3–7.9; head width 3.2–3.4; head length 2.5–2.6; intertegular distance 2.2–2.4; forewing length 6.7–7.1.

*Colouration*: Marginal zone of T1 dark-brown. Marginal zone of T6 pale-brown.

*Structure*: Clypeal mid-longitudinal area more shallowly depressed. Malar area ~2.4x as long as basal depth of mandible (58:24). F1 ~1.3x as long as its apical width (28:22). UID:LID (73:64). Horizontal surface of metapostnotum ~0.5x as long as metanotum (19:42). Hind basitarsus ~3.5x longer than broad (53:15). Outer rami of hind tarsal claws ~1.7x as long as inner rami (24:14). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 32A, 32B, 32C, respectively.

*Pubescence*: Mesepisternum with off-white and black hairs intermingled. Appressed hairs on metasomal terga restricted to marginal zones of T1–T5. Setae on T4–T5 pale-yellow. S2 with plumose hairs. Marginal zones of S2–S5 with pale-yellow, plumose, suberect, short hairs (except moderately short on S2).

*Surface sculpture*: Supraclypeal area densely punctate (except mid-longitudinal band impunctate). Mesoscutum moderately densely punctate throughout. Scutellum coarsely punctate. T2–T3 moderately finely punctate. T4–T6 with rugulose interspaces.



**Figure 32.** Dorsal view of the male terminalia of *C. gilvus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** *Primary type specimens:* Lectotype ♀ of *C. gilvus* – “Chili; Arica”. “Colletes; gilvus; ♀ Vach”. “MUSEUM PARIS; COLL. J. VACHAL 1911”. “LECTOTYPE”.

“LECTOTYPE; *Colletes gilvus* ♀; Vachal, 1909; designated R. Ferrari, 2017”. {MNHP}.

**[hereby designated].** Lectotype ♀ of *C. tomentosus* – “Chile; Arica; 1890”. “Colletes; tomentosus; 1909 Friese det.”. “Type”. “Coll.; Friese”. “Zool. Mus.; Berlin”. “LECTOTYPE; *Colletes tomentosus*; Friese, 1910; lab. Melo, 2015”. “<http://coll.mfn-berlin.de/u/; 58f9c7>”. {ZMB}.

*Secondary type specimens:* Paralectotypes ♂♂ of *C. gilvus* – **CHILE – Region XV:** Arica, 2♂♂, {MNHP}.

*Additional specimens:* **CHILE – Region XV:** 1.5km SE of Campamento Planchones, (-18.698, -69.608), 3065m, 31/i/2013, [Postlethwaite & Monckton], 3♀♀, {PCYU}; idem, except 17/iv/2013, [Monckton & Postlewaite], 10♀♀; idem, except 24/ix/2013, 2♀♀1♂; idem, except 31/x/2013, [Monckton & Postlethwaite], 3♀♀. 11km S of Putre, (-18.271, -69.572), 3559m, 14/iv/2004, [L.Packer], 3♀♀2♂♂, {PCYU}. 30km W of Zapahuira, (-18.333, -69.894), 1799m, 3/iv/2000, [L.Packer], 4♀♀5♂♂, {PCYU}. Belén, (-18.467, -69.513), 3295m, 18/vii/1976, [Porter, Calmbacher & Vargas], 1♀, {KUNHM}; idem, except 18/vii/1976, [Porter & Calmbacher], 1♀, {AMNH}. Central Hidroeléctrica Chapiquiña, (-18.386, -69.553), 3460m, 9/iv/2000, [L.Packer], 1♀2♂♂, {PCYU}. E of Putre, (-18.190, -69.520), 4141m, 15/iv/2004, [L.Packer], 1♀1♂, {PCYU}. Estación Regadio, (-18.456, -69.500), 3507m, 19/iv/2004, [L.Packer], 1♀, {PCYU}. Highway CH-11 km 116.5, (-18.245, -69.554), 3549m, 3/xi/2013,

[S.Monckton], 5♀♀3♂♂, {PCYU}. Highway A-31 km 164, (-18.356, -69.548), 3620m, 1/xi/2013, [S.Monckton], 5♀♀, {PCYU}. Mirador de Socoroma, (-18.279, -69.584), 3414m, 15/xi/1997, [L.Packer], 1♂, {PCYU}. Murmuntani, (-18.532, -69.563), 3421m, iv/2004, [L.Packer], 1♂, {RPSP}. N of Zapahuira, (-18.325, -69.587), 3405m, 22/iv/2013, [Postlethwaite & Monckton], 1♂, {PCYU}; idem, except 29/iv/2015, [L.Packer], 4♂♂. NW of Belén, (-18.452, -69.514), 3446m, 28/xi/2013, [Postlethwaite & Monckton], 2♀♀, {PCYU}. Pampa Oxaya, (-18.700, -69.612), 3069m, 20/iv/2012, [L.Packer], 1♂, {PCYU}. Quebrada Cardones, (-18.438, -69.741), 2728m, 8/xi/2014, [L.Packer], 1♀, {PCYU}. Road to Cobija, (-18.718, -69.609), 3132m, 18/iv/2013, [Postlethwaite & Monckton], 1♀, {PCYU}. S of Chapiquiña, (-18.399, -69.536), 3351m, 24/ix/2013, [L.Packer], 1♀3♂, {PCYU}. S of Putre, (-18.413, -69.669), 3046m, 3/ii/2013, [Postlethwaite & Monckton], 2♂♂, {PCYU}. SE of Zapahuira, (-18.346, -69.552), 3559m, 13/iv/2004, [L.Packer], 2♂♂, {PCYU}. Socoroma, (-18.263, -69.601), 3070m, iv/1997, [G.Castillo], 1♂, {AMNH}. Tambo, (-18.356, -69.620), 3235m, 4/iv/2000, [L.Packer], 2♂♂, {PCYU}; idem, except 12/iv/2004, 1♀; idem, except 17/iv/2012, 1♂. Tignamar, (-18.567, -69.488), 3416m, 24/ix/2013, [Postlethwaite & Monckton], 3♀♀, {PCYU}. Timar, (-18.487, -70.317), 115m, 10/vii/1976, [Porter & Calmbacher], 4♂♂, {AMNH}; idem, except 24/ix/2013, [Postlethwaite & Monckton], 2♀♀3♂♂, {PCYU}. Tojo Tojone, (-18.485, -69.528), 3150m, 24/ix/2013, [L.Packer], 1♀, {PCYU}. W of Zapahuira, (-18.457, -69.773), 2459m, iv/2004, [L.Packer], 2♂♂, {PCYU}. Zapahuira, (-18.341, -69.595), 3328m, 17/iv/2012, [L.Packer], 3♂♂, {PCYU}. **Region I:** 12km SW of Chusmiza, (-19.751, -69.257), 3002m, 21/ix/2013, [Almeida & Packer], 6♀♀1♂, {RPSP}; idem, except [L.Packer], 9♀♀2♂♂, {PCYU}. 73km SE of Pozo Almonte, (-20.312, -69.129), 3188m, 27/iv/2013, [Postlethwaite & Monckton], 10♂♂, {PCYU}. 82km NE of Huara, (-19.673, -69.179), 3432m, 21/ix/2013, [Almeida & Packer], 1♂, {RPSP}. Chusmiza, (-19.751, -69.257), 3002m, 11/iv/2004, [L.Packer], 1♀2♂♂, {PCYU}; idem, except 11/iv/2014, 2♀♀; idem, except 21/ix/2013, [Postlethwaite & Monckton], 2♀♀; idem, except 29/x/2013, [Postlethwaite & Monckton], 1♀. E of Huara, (-19.744, -69.245), 3097m, 25/xi/2013, [Postlethwaite & Monckton], 1♂, {PCYU}. Highway CH-15 km 62.6, (-19.753, -69.260), 2985m, 14/iv/2013, [Postlethwaite & Monckton], 3♂♂, {PCYU}; idem, except km 63, (-19.751, -69.257), 3002m, 30/x/2013, [S.Monckton], 2♀♀3♂♂; idem, except km 64.5, (-19.744, -69.245), 3097m, 25/xi/2013, 7♀♀; idem, except km 73.3, (-19.687, -69.194), 3446m, 5♀♀1♂. Mamiña, (-20.076, -69.204), 2800m, 6/iv/2013, [Postlethwaite & Monckton], 1♀7♂♂, {PCYU}.

Road to Mamiña, (-20.072, -69.183), 2898m, 6/iv/2013, [Postlethwaite & Monckton], 2♂♂, {PCYU}. SE of Pozo Almonte, (-20.303, -69.043), 3976m, 28/x/2013, [Monckton & Postlethwaite], 1♀, {PCYU}. Usmagama, (-19.742, -69.219), 2888m, 11/iv/2004, [L.Packer], 1♀3♂♂, {PCYU}. W of Pozo Almonte, (-20.302, -69.094), 3545m, 11/iv/2013, [Postlethwaite & Monckton], 1♂, {PCYU}. Yala-yala, (-19.301, -69.368), 3021m, 11/iv/2004, [L.Packer], 1♂, {PCYU}. **Region II:** 5km E of Aguas Blancas, (-23.329, -67.950), 2762m, 7/iv/2004, [L.Packer], 3♀♀1♂, {PCYU}. Aguas Blancas, (-23.267, -67.997), 2470m, 12/x/2001, [Packer & Fraser], 1♀, {PCYU}. E of San Pedro, (-22.911, -67.932), 3587m, 22/x/2015, [L.Packer], 2♀♀1♂, {PCYU}. Highway 23 km 175, 12/x/2001, [Packer & Fraser], 1♀, {PCYU}. Highway CH-27 km 17, (-22.913, -68.026), 2871m, 26/x/2013, [S.Monckton], 1♂, {PCYU}. N of San Pedro Atacama, (-22.766, -68.070), 3208m, 20/xi/2013, [Postlethwaite & Monckton], 2♀♀, {PCYU}. NW of San Pedro de Atacama, (-22.768, -68.387), 3318m, 28/iv/2013, [Postlethwaite & Monckton], 1♀, {PCYU}. Road to Machuca km 5.4, (-22.724, -68.054), 3511m, 27/x/2013, [L.Packer], 1♂, {PCYU}. Road to Matancilla, (-22.665, -68.230), 3079m, 21/xi/2013, [Postlethwaite & Monckton], 1♂, {PCYU}. San Pedro de Atacama, (-22.766, -68.070), 3208m, 6/xii/2013, [J.Postlethwaite], 1♀, {PCYU}. Talabre, (-23.290, -67.940), 2899m, [L.Packer], 2♀♀, {PCYU}.

**Range:** Chile (Regions XV, I, II). See also Fig. 30A.

**Biogeographic distribution:** South American transition zone: Desert and Atacama provinces. Northern Chilean species distributed in the summer rainfall area at altitudes of 2300–4200m a.s.l.

**DNA barcode:** Available. BOLD: AAJ7575 (7♀♀4♂♂). Distance from the nearest neighbour (*C. sulcatus*): 9.36–9.98%.

**Floral hosts:** Leguminosae – *Caesalpinia* sp. (Toro 1999); *Medicago sativa* L. (Toro 1999); *Prosopis* sp. (Toro 1999). Malvaceae – *Tarasa operculata* (Cav.) Krapov (this study).



**Comments:** *Colletes gilvus* is one the most common species found in northern Chile. Its type series consists of three specimens, one female and two males, which were labelled as lectotype and paralectotypes, respectively, by Moure in 1986 (A. Touret-Alby, *pers. comm.*). This designation, however, cannot be considered valid, as specimen labels do not constitute published work according to the Code, and therefore do not satisfy its criteria of valid nomenclatural acts (ICZN 1999; Article 9.8). Therefore, I herein formally designate the female (the same specimen chosen by Moure) as the species' lectotype (see "Material studied", above).

All specimens of *C. gilvus* that I studied were caught at altitudes above 2200m a.s.l., except for those belonging to the type series, which were supposedly collected in the city of Arica (Region XV) located at the coast (see "Material studied", above). Given the uniqueness of that record and the enormous incompatibility with the other data, it appears very unlikely that the type series was actually collected at such low altitude. Therefore, the biogeographic information provided herein on *C. gilvus* does not take the supposed occurrence in Arica into consideration; likewise, this record is not plotted onto the distribution map (Fig. 30A).

Two additional remarks about the type series of *C. gilvus* should be made. First, it contains more than one species, as one of the male specimens actually belongs to *C. atacamensis*. According to the Code, this specimen must still be considered a valid syntype of *C. gilvus*, which prompted me to designate it as a paralectotype, even though I have also labelled it as *C. atacamensis* (ICZN 1999; Article 72.4.2). Second, Moure also added a paralectotype label to an additional female specimen the identity of which Vachal was not sure about (free translation from French): "One specimen collected by Gay, from Coquimbo (Chile), looks to me as *Colletes hirta* Spin. (not Lep.)" (Vachal 1909: 57). According to the Code, the type series of a nominal species must include no specimen doubtfully attributed to the particular species by the author (ICZN 1999; Article 72.4.1). Therefore, the female specimen labelled by Moure, which actually belongs to *C. sulcatus*, must not be considered a valid paralectotype of *C. gilvus*.

Examination of the female lectotype of *C. tomentosus* confirmed that this species is a junior synonym of *C. gilvus*, as previously proposed by Toro (1999: 28). This synonymy, however, was not acknowledged by Moure & Urban (2002) and Moure *et al.* (2007).

***Colletes guanta* Rojas & Toro, 1993**

(Figs. 33A–C)

*Colletes guanta* Rojas & Toro, 1993: 84; Toro 1999: 29; Moure *et al.* 2007: 682; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

Holotype ♀ (examined). {AMNH}.

**Diagnosis:** The following combination of characters is sufficient to separate *C. guanta* from all other *Colletes* species found in Chile: clypeal mid-longitudinal area carinate, mesoscutal pubescence pale-yellow, hind tibia dark-brown, and metasomal terga metallic blue.

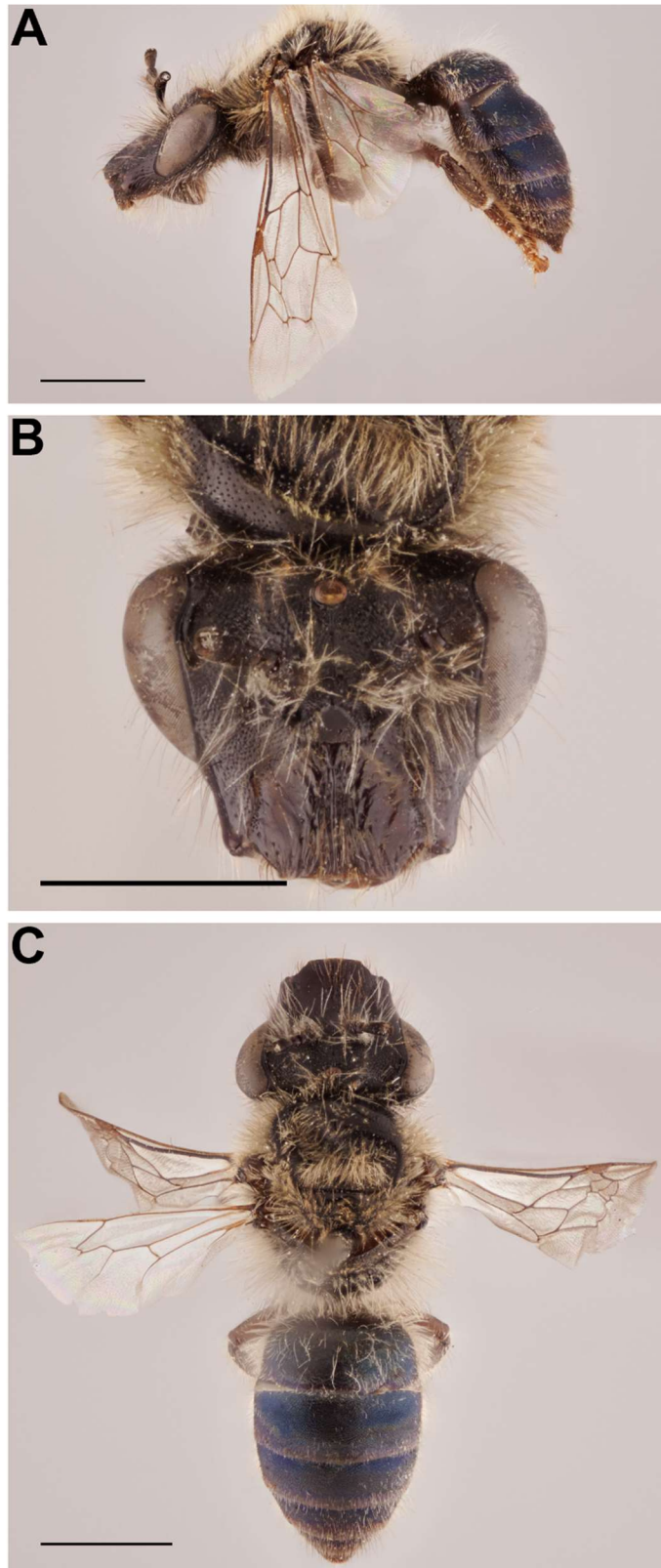
*Colletes guanta* is most similar to *C. quehu*, however, the females (males of both species remain unknown) of these species can be distinguished by the comparatively longer malar area, 1.8x as long as basal depth of mandible, in *C. guanta* (malar area 1.5x as long as basal depth of mandible in *C. quehu*); comparatively shorter F1, ~1.2x as long as its apical width, in *C. guanta* (F1 ~1.4x as long as its apical width in *C. quehu*); and hind tibia dark-brown in *C. guanta* (hind tibia pale-orange in *C. quehu*).

**Redescription:** FEMALE (Figs. 33A, 33C, 33E):

*Dimensions (mm):* Approximate body length 7.4–7.6; head width 3.0–3.1; head length 2.3; intertegular distance 2.1–2.2; forewing length 6.0–6.1.

*Colouration:* Black except metallic blue on metasomal terga (discs also with greenish hues); marginal zones metallic purplish. Dark-brown on tegula, vein R of forewing, legs (except pale-brown on tarsomeres 2–5), metasomal sterna (discs of S2–S5 with metallic dark-blue hues). Pale-brown on wing veins, stigma, tibial spurs, distal half of tarsal claws. Pale-yellow on proximal half of tarsal claws, marginal zones of metasomal sterna. Reddish-brown marked on distal half of mandible.

*Structure:* Labrum medially flat and without ridges. Clypeal mid-longitudinal area with a strong carina on lower 3/4; adjacent area declivous. Malar area 1.8x as long as basal depth of mandible (45:25). F1 ~1.2x as long as its apical width (34:28). UID:LID (67:66). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded.



**Figure 33.** *Colletes guanta* Rojas & Toro, 1993. Female: (A) habitus, lateral view; (B) face, frontal view; (C) habitus, dorsal view. Scale bars = 2mm.

Horizontal surface of metapostnotum  $\sim 0.6x$  as long as metanotum (21:36); metapostnotal pits poorly-delimited; posterior transverse carina sinuous and interrupted medially. Posteromedial surface of front coxa bearing very short spine ( $0.3x$  MOD). Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 3.5x$  longer than broad (53:15). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Pale-yellow, plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, interantennal, frontal and genal areas (except long near proboscidal fossa), pronotal lobe, mesoscutum, scutellum, metanotum, posteroventral surface of front trochanter and femur, ventral surface of mid and hind trochanters, ventral margin of mid femur, S1; such hairs long on upper margin of lateral surface of propodeum, T1. Paraocular area with pale-yellow and black hairs intermixed. Pale-yellow, erect, moderately short setae on mandible; such hairs long on posterior surface of tibiae (except very long on hind tibia). Fulvous, suberect, short setae on dorsal surface front and mid tibiae; such setae pale-yellow, thick on ventral surface of mid and hind tarsi (thickest towards distal margin). Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T2–T5 and S3–S6 covered with pale-yellow, erect, short setae (except moderately short on T5 and lateral areas of T3–T4); T2 also with plumose hairs. S2 with pale-yellow, erect, moderately short hairs, which are branched only apically.

*Surface sculpture:* Clypeus longitudinally striate on lower  $1/4$  and near mid-longitudinal carina; smooth and shiny elsewhere. Malar area with sparse, moderately fine punctures medially; interspaces smooth. Supraclypeal area rugulose below; smooth above. Paraocular area punctures crowded and moderately fine below; dense and fine above (sparsest at antennal socket level); interspaces smooth throughout. Frontal area densely and moderately finely punctate; interspaces rugulose. Vertexal area sparsely and minutely punctate near eye (interspaces smooth); densely and finely punctate medially (interspaces imbricate); rugose near ocellus. Mesoscutum and scutellum moderately finely punctate; moderately densely punctate on former (except sparsely punctate on mid-posterior area), densely punctate on latter; interspaces smooth (except rugulose on scutellar posterior  $1/4$ ). Metanotum densely and finely punctate; interspaces rugulose. Mesepisternum moderately sparsely and moderately finely punctate; interspaces imbricate. Metepisternum rugulose above and below; obliquely striate medially. Lateral surface of propodeum imbricate. Upper area of vertical surface of metapostnotum rugose medially.

Metasomal terga finely punctate; T1 sparsely punctate; T2–T5 densely punctate; interspaces imbricate throughout. Metasomal sterna finely and moderately sparsely punctate (except moderately finely punctate on S6 mid-longitudinally).

MALE: Unknown.

**Material studied:** *Primary type specimen:* Holotype ♀ – “HOLO; TIPO”. “CHILE Coquimbo; Baños del Toro; 14 I ’56 3,350m.; (Wagenknecht)”. “Colletes; guanta n.sp; Toro & Rojas 93”. “AMNH\_IZC 000324329”. {AMNH}.

*Additional specimen:* **CHILE – Region IV:** Baños del Toro, (-29.837, -70.026), 3350m, i/1988, [R.Solar], 1♀, {AMNH}.

**Range:** Chile (Region IV). See also Fig. 3B.

**Biogeographic distribution:** Andean region: Central Chilean sub-region (Coquimban province). Central Chilean species found at altitudes above 3300m a.s.l.

**DNA barcode:** Unavailable.

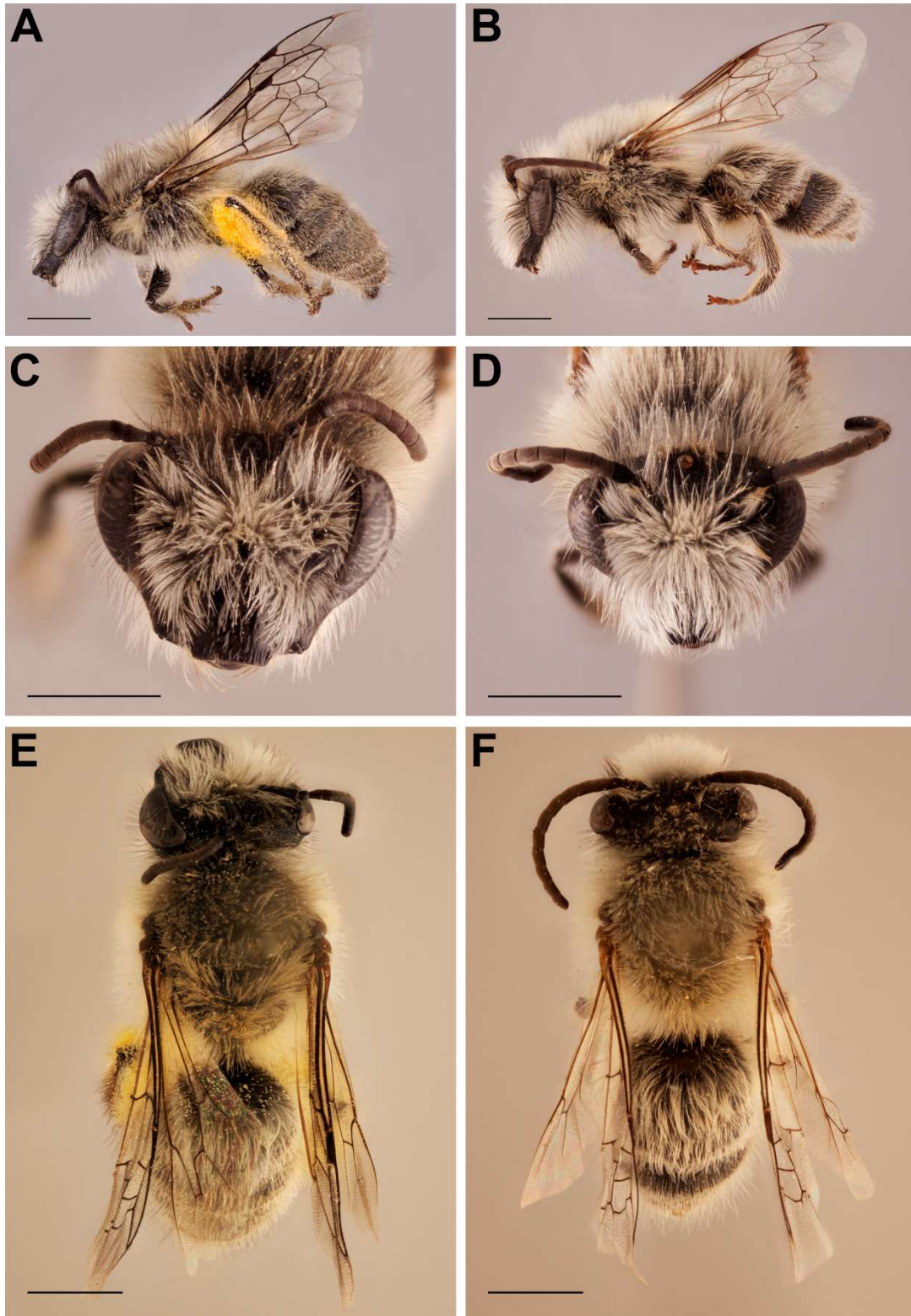
**Floral hosts:** Unknown.

**Comments:** Extremely rare species known only from its type locality (Baños del Toro, Region IV). The male remains unknown.

***Colletes kuhlmanni* Ferrari, new species**

(Figs. 34A–F)

**Diagnosis:** The combination of pubescence mostly pale-yellow, malar area 1.2x as long as basal depth of mandible, paraocular area with longitudinal band of black hairs, posterior hind tibial spur ciliate, and T1 sparsely and minutely punctate is sufficient to distinguish *C. kuhlmanni* n. sp. from all other species of the genus found in Chile.



**Figure 34.** *Colletes kuhlmanni* Ferrari, **n. sp.** Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.



*Colletes kuhlmanni* **n. sp.** is most similar to *C. gilvus*, but these species can be differentiated by T1 sparsely and minutely punctate in *C. kuhlmanni* **n. sp.** (T1 moderately densely and finely punctate in *C. gilvus*). Additionally, the female of these species differ in the disc of T1, which is covered only with erect long hairs in *C. kuhlmanni* **n. sp.** (T1 with erect long and sparse appressed hairs in female *C. gilvus*). Also, F1 is approximately as long as its apical width in male *C. kuhlmanni* **n. sp.** (F1 ~1.3x as long as its apical width in *C. gilvus*).

**Description: FEMALE** (Figs. 34A, 34C, 31F):

*Dimensions (mm)*: Approximate body length 11.0; head width 3.5; head length 2.7; intertegular distance 2.8; forewing length 7.3.

*Colouration*: Black except reddish-brown marked on distal 1/3 of mandible. Dark-brown on tegula, wing veins (except vein R of forewing black), distitarsi (except distal 1/5 pale-brown), distal half of tarsal claws, marginal zones of T1–T5. Pale-brown on proximal half of tarsal claws. Pale-yellow on tibial spurs, marginal zones of S1–S5.

*Structure*: Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area narrowly (0.4x MOD) and deeply depressed on upper half; depression broad and shallow on lower half; adjacent lateral area convex; apicomedial ridge absent. Malar area ~1.2x basal depth of mandible (34:28). F1 ~1.7x as long as its apical width (40:23). UID:LID (69:60). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum 0.45x as long as metanotum (28:62); metapostnotal pits well-delimited; posterior transverse carina straight and narrowly interrupted medially. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus 3.6x longer than broad (54:15). Outer rami of hind tarsal claws ~2x as long as inner rami (30:16). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence*: Pale-yellow, plumose, erect, long on lateral slopes of clypeus and supraclypeal area, interantennal area, coxae, trochanters (except very short on dorsal surface), ventral surface of femora, S1; such hairs very long on genal area (progressively shorter towards outer margin of compound eye), mesepisternum, metepisternum, superior margin of lateral surface of propodeum, T1. Mixed pale-yellow and black, plumose, erect, long hairs on paraocular and vertexal areas, mesoscutum, scutellum, metanotum. Pale-yellow, suberect,

moderately long setae on mandible, dorsal surface of mid and hind basitarsi and tibiae. Pale-yellow, erect, very long setae on posterior margin of mid and hind basitarsi; thick setae on ventral surface of mid and hind tarsi (thickest towards distal margin). Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T2–T5 with pale-yellow, dense, appressed hairs (T4–T5 also with black, erect, long setae). Posterior 1/3 of S3–S5 covered with setae and plumose hairs intermixed. S2 with pale-yellow, erect, short hairs, which are branched only apically.

*Surface sculpture:* Clypeus shiny throughout; mid-longitudinal depression densely and finely punctate; adjacent convex area smooth on upper 3/4, lower 1/4 longitudinally striate. Malar area longitudinally striate. Supraclypeal area with very sparse moderately coarse punctures; interspaces smooth and shiny. Paraocular area densely and moderately coarsely punctate below (sparser and coarser towards supraclypeal area); punctures crowded and moderately fine above; interspaces smooth and shiny throughout. Frontal area punctures crowded; interspaces rugose and dull. Vertexal punctation dense with moderately fine punctures intermingled with coarse ones; interspaces smooth and shiny. Mesoscutum coarsely punctate; densely punctate on anterior and lateral areas; sparsely punctate on mid-posterior area. Scutellar disc densely punctate; posterior margin punctures crowded. Mesepisternum coarsely punctate; densely punctate anteriorly to episternal groove; slightly sparser posteriorly to groove. Mesoscutal, scutellar, and mesepisternal interspaces smooth and shiny throughout. Metanotum punctures crowded; interspaces rugulose but somewhat shiny. Metepisternum obliquely striate medially; rugulose above. Lateral surface of propodeum rugulose; punctation difficult to spot. Upper area of vertical surface of metapostnotum smooth medially. Metasomal terga sparsely and minutely punctate; interspaces smooth and shiny throughout. Metasoma sterna finely and shallowly punctate; densest posterolaterally; interspaces imbricate.

MALE (Figs. 34B, 34D, 34F). As in female, except for usual secondary sexual characteristics and as follows:

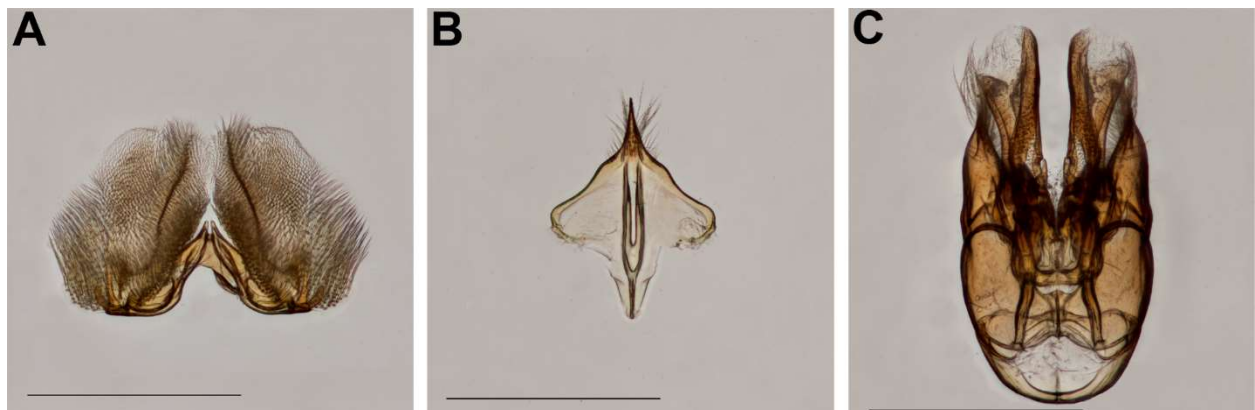
*Dimensions (mm):* Approximate body length 8.2; head width 3.2; head length 2.6; intertegular distance 2.1; forewing length 6.9.

*Colouration:* Posterior margins of S1–S5 pale-brown.

*Structure:* Clypeal mid-longitudinal depression evenly narrow and deep throughout. Malar area 2.3x basal depth of mandible (46:20). F1 1.1x as long as its apical width (32:29). UID:LID (72:59). Horizontal surface of metapostnotum 0.4x as long as metanotum (16:40); posterior transverse carina somewhat sinuous. Hind basitarsus 3.1x longer than broad (55:18). Outer rami of hind tarsal claws 1.75x as long as inner rami (28:16). S7, S8 and genital capsule as in Figs. 35A, 35B, 35C, respectively.

*Pubescence:* Mesoscutum, scutellum and metanotum without black hairs. Metasomal appressed pubescence restricted to marginal zones; discs of T2–T3 covered with plumose, erect, moderately long hairs; discs of T4–T5 with long setae.

*Surface sculpture:* Clypeal convex area smooth throughout, without sulci. Supraclypeal area densely punctate. Scutellar interspaces rugulose. Mesepisternum, anteriorly to episternal groove, with rugulose interspaces. T3–T5 moderately densely punctate.



**Figure 35.** Dorsal view of the male terminalia of *C. kuhlmanni* n. sp. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Type material:** *Holotype* ♀ – “CHILE Region Metro; Farellones 2179m; S33.35627 W70.32478; 9.i.2009 L. Packer Brassicaceae; PCYU CHI09-11-1-011”. “HOLOTYPE; *Colletes kuhlmanni* ♀; Ferrari, new species”. {PCYU}.

*Paratypes:* **CHILE – Region II:** Cifuncho, (-25.657, -70.632), 58m, 29/ix/1994, [E.Chiapa], 1♂, {PUCV}; idem, except 09/i/1996, 1♀1♂; idem, except [H.Toro], 1♂. N of

Quebrada de Taltal, (-25.456, -70.445), 308m, 2/x/1994, [E. Chiappa], 1♂, {PUCV}. Quebrada de Taltal, (-25.488, -70.424), 502m, 20/x/1993, [H.Toro], 1♂, {PUCV}; idem, except 31/x/1993, [H.Chiappa], 1♂. **Region III:** 2.5km E of Diego de Almagro, (-26.394, -70.059), 772m, 17/x/2010, [Packer & Almeida], 6♂♂, {PCYU}; idem, except 2♂♂, {RPSP}; idem, except 4km E of Diego de Almagro, (-26.367, -70.006), 871m, 2♂♂, {RPSP}. 7.3km W of Domeyko, (-28.978, -70.964), 662m, 22/v/2010, [Packer & Almeida], 3♂♂, {PCYU}; idem, except 22/x/2010, [L.Packer], 1♂. 15.5km NNE of El Algarrobal, (-28.018, -70.553), 662m, 13/x/2010, [Almeida & Packer], 1♀, {RPSP}. 19km N of Vallenar, (-28.414, -70.721), 663m, 13/x/2010, [Almeida & Packer], 1♂, {RPSP}. 37km W of Copiapó, (-27.350, -70.000), 1051m, 16/xi/2003, [M.Irwin], 1♂, {BBSL}. 40km SE of Caldera, (-18.578, -69.943), 846m, 16/x/1957, [L.Peña], 1♂, {KUNHM}. 125km SE of Copiapó, (-28.221, -69.643), 3289m, 9/xi/2003, [Irwin & Parker], 4♀♀5♂♂, {BBSL}. Embalse Lautaro, (-27.984, -69.987), 1174m, 30/ix/2013, [L.Packer], 2♀♀1♂, {PCYU}. N of Vallenar, (-28.490, -70.735), 571m, 11/x/2000, [L.Packer], 2♀♀8♂♂, {PCYU}. NE of Aguada de Tongoy, (-28.512, -71.166), 120m, 14/ix/2010, [L.Packer] 1♂, {PCYU}. Potrerillos, (-26.427, -69.482), 2743m, 19/x/2015, [L.Packer], 1♂, {PCYU}. Puente Río Potro, (-28.275, -69.735), 2564m, 21/v/2010, [L.Packer], 1♂, {PCYU}; idem, except 21/x/2010. Quebrada del Potrero, (-26.856, -70.663), 357m, 1/v/2010, [L.Packer], 1♂, {PCYU}. Road to Mina Caserones, (-28.174, -69.803), 1848m, 30/ix/2013, [L.Packer], 1♀, {PCYU}. S of Agua Dulce, (-26.404, -69.585), 1924m, 16/xi/2013, [Monckton & Postlethwaite], 1♀, {PCYU}. S of Cachiuyo, (-29.147, -70.941), 1204m, 9/v/2010, [L.Packer], 1♂, {PCYU}. S of Freirina, (-28.544, -71.053), 264m, 14/ix/2010, [L.Packer], 1♂, {PCYU}. SE of Copiapó, (-27.765, -70.159), 840m, 29/ix/2013, [L.Packer], 1♂, {PCYU}. W of Domeyko, (-28.972, -71.000), 617m, 5/x/2010, [Packer & Fraser], 1♂, {PCYU}. W of Finca Los Salinas, (-27.660, -69.894), 1752m, 4/ii/2016, [L.Packer], 3♂♂, {PCYU}. **Region IV:** 1km E of Parque Nacional Fray Jorge, (-30.637, -71.597), 259m, 15/x/2000, [L.Packer], 2♀♀, {PCYU}. 7km N of La Higuera, (-29.444, -71.194), 375m, 14/iv/2000, [L.Packer], 1♂, {PCYU}; idem, except 30km N of la Higuera, (-29.276, -71.036), 624m, 3♀♀; idem, except SW of La Higuera, 1♂. 7km N of Los Vilos, (-31.849, -71.493), 75m, 11/x/2003, [M.Irwin], 2♀♀, {BBSL}; idem, except 25/xii/2003, [Parker & Irwin], 1♂. 15km S of La Villa, (-30.104, -70.990), 470m, 21/xi/2003, [Irwin & Parker], 1♀, {BBSL}. Caleta Los Hornos, (-29.620, -71.287), 5m, 11/xi/1997, [L.Packer], 1♀, {PCYU}. Caleta Los Lobos, (-31.901, -71.497), 10m, 26/x/2001, [Packer & Fraser], 1♀, {PCYU}. E of

Aduanas, (-30.138, -70.061), 2707m, 3/ii/2016, [L.Packer], 3♂♂, {PCYU}. El Peñon, (-30.132, -71.216), 208m, 11/ix/1956, [R.Wagenknecht], 1♂, {KUNHM}. Guampulla, (-30.429, -70.977), 562m, 19/x/2001, [Packer & Fraser], 1♀, {PCYU}. Highway 41 km 139, 5/xi/2015, [L.Packer], 2♀♀, {PCYU}. La Serena, (-29.896, -71.253), 15m, 25/xi/1957, [Wagenknecht], 1♀, {PCYU}. Los Corrales, (-30.188, -69.911), 3842m, 3/ii/2016, [L.Packer], 6♂♂, {PCYU}. N of Hurtado, (-30.266, -70.660), 1342m, 16/x/2013, [S.Monckton], 5♀♀1♂, {PCYU}. N of La Serena, (-29.862, -71.251), 23m, 8/xi/2001, [L.Packer], 1♀, {PCYU}. Puente Mata Gorda, (-31.903, -71.489), 31m, 16/xii/2013, [Postlethwaite & Monckton], 1♀1♂, {PCYU}. Rivadavia, (-29.975, -70.551), 903m, 16/v/1958, [R.Wagenknecht], 1♂, {KUNHM}. S of Los Vilos, (-31.931, -71.513), 15m, 10/xii/2013, [S.Monckton], 1♀, {PCYU}. SE of Los Choros, (-29.305, -71.283), 136m, 13/ix/2010, [L.Packer], 3♀♀, {PCYU}. Parque Nacional Fray Jorge, (-30.637, -71.597), 259m, 15/iv/2000, [L.Packer], 1♀8♂♂, {PCYU}; idem, except 14/x/2000, 2♀♀; idem, except 21/x/2001, [Packer & Fraser], 1♂. Portezuelo Tres Cruces, (-30.216, -70.651), 1963m, 31/x/1957, [L.Peña], 1♂, {KUNHM}. Quebrada Seca, (-30.334, -71.265), 729m, 11/x/2002, [Grixti & Zayed], 1♀, {PCYU}. **Region V:** E of Río Blanco, (-32.875, -70.208), 1949m, 30/xii/2008, [L.Packer], 6♀♀3♂♂, {PCYU}. La Campana National Park, (-32.952, -71.073), 621m, 10/i/2000, [M.Irwin], 1♀, {PCYU}. Portillo, (-32.850, -70.133), 2612m, 30/xii/2009, [L.Packer], 1♀, {PCYU}. **Region Metropolitana:** Cerro El Roble, (-32.976, -71.013), 2202m, 1/i/2009, [L.Packer], 1♀4♂♂, {PCYU}. Cuna Gallego Valley, (-32.882, -70.137), 2286m, 10/i/2009, [L.Packer], 1♀5♂♂, {PCYU}. E of El Volcán, (-33.483, -70.040), 1994m, 7/i/2009, [L.Packer], 2♀♀2♂♂, {PCYU}. El Manzano, (-33.439, -70.634), 489m, 18/i/1975, [Magunacelaya], 1♂, {PUCV}. Farellones, (-33.356, -70.324), 2179m, 9/i/2009, [L.Packer], 1♀5♂♂, {PCYU}; idem, except 31/xii/2008, 4♀♀3♂♂; idem, except 9/ii/2001, [E.Arias], 1♂. Valle Nevado, (-33.362, -70.257), 2663m, 31/xii/2008, [L.Packer], 1♂, {PCYU}.

**Range:** Chile (Regions II–Metropolitana). See also Fig. 30B.

**Biogeographic distribution:** Andean region: Central Chilean sub-region (Coquimban and Santiaguan provinces). Central Chilean species found at altitudes of 0–3900m a.s.l.

**DNA barcode:** Available. BOLD BIN: AAO3265 (5♀♀6♂♂). Distance from the nearest neighbour (*C. atacamensis*): 10.34–11.06%.

**Floral hosts:** Boraginaceae – *Phacelia* sp. Compositae – *Baccharis* sp.; *Solidago* sp. Portulacaceae – *Cistanthe salsoloides* (Barnéoud) Carolin ex M. A. Hershkovitz. Solanaceae – *Nolana* sp. Some of the following records, which were originally attributed to *C. gilvus* by Toro (1999), may also apply to *C. kuhlmanni* **n. sp.**: Leguminosae – *Caesalpinia* sp.; *Medicago sativa* L.; *Prosopis* sp.

**Etymology:** This species is named after the melittologist Michael Kuhlmann in recognition of his profound dedication to the study of the genus *Colletes*.

**Comments:** Very common species distributed in northern and central Chile. Females visit flowers of, at least, seven different plant families.

### ***Colletes longiceps* Friese, 1910**

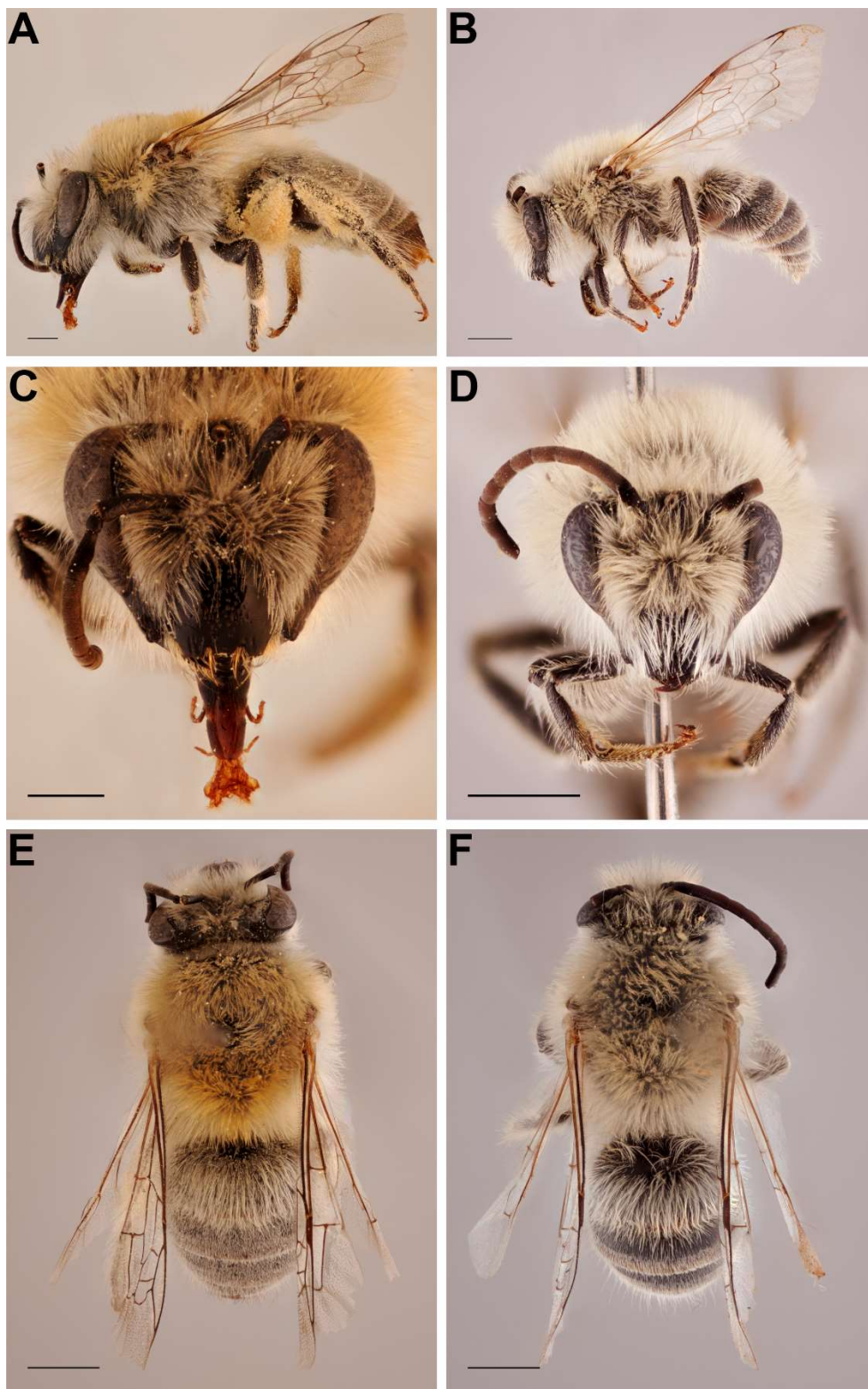
(Figs. 36A–F)

*Colletes longiceps* Friese, 1910: 649, 1912: 366; Cockerell 1926: 302; Jaffuel & Pirion 1926: 364; Toro 1986: 122, 1999: 29; Moure & Urban 2002: 12; Moure *et al.* 2007: 683; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

Lectotype ♂ (examined) designated by Moure & Urban (2002: 12). {ZMB}.

**Diagnosis:** The female *C. longiceps* is recognizable by having the combination of the following characteristics: clypeal mid-longitudinal area not depressed, paraocular area and mesosomal dorsum with pale-yellow hairs only, posterior hind tibial spur pectinate, and T1–T5 covered with pale-yellow, dense appressed hairs. Males are diagnosable by having the upper area of vertical surface of metapostnotum projected posteriorly in relation to horizontal surface, and T7 apex acute.





**Figure 36.** *Colletes longiceps* Fries, 1910. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

*Colletes longiceps* is very similar to *C. sulcatus*, but their females can be differentiated by the clypeal mid-longitudinal area not depressed in the former (clypeal mid-longitudinal area deeply depressed in the latter); and posterior hind tibial spur pectinate in *C. longiceps* (spur ciliate in *C. sulcatus*). The males can be distinguished by the paraocular area with only pale-yellow hairs in *C. longiceps* (paraocular area with pale-yellow and black hairs intermixed, in *C. sulcatus*); and mesepisternal interspaces rugulose in *C. longiceps* (mesepisternal interspaces smooth in *C. sulcatus*).

**Redescription: FEMALE** (Figs. 36A, 36C, 36E):

*Dimensions (mm)*: Approximate body length 10.3–11.5; head width 3.4–3.8; head length 2.5–2.7; intertegular distance 3.1–3.5; forewing length 7.8–8.4.

*Colouration*: Black except pale-brown on tegula, wing veins (except vein R of forewing black), dorsal surface of distitarsi, stigma, marginal zones of T1–T5, posterior half of mid-longitudinal band of S6. Reddish-brown on distal half of tarsal claws; marked on distal 1/3 of mandible. Dark-brown on dorsal surface of flagellum, dorsal surface of mediotarsi. Pale-yellow on tibial spurs, proximal half of tarsal claws, marginal zones of S1–S5.

*Structure*: Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area not depressed; adjacent lateral area convex; apicomedial ridge absent. Malar area subequal to basal depth of mandible (41:39). F1 ~1.5x as long as its apical width (34:22). UID:LID (73:70). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded. Horizontal surface of metapostnotum nearly half as long as metanotum (20:44); metapostnotal pits well-delimited; posterior transverse carina barely visible. Posteromedial surface of front coxa with very long spine (0.7x MOD). Posterior hind tibial spur pectinate. Hind basitarsus ~3.7x longer than broad (60:16). Outer rami of hind tarsal claws 2x as long as inner rami (20:10). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence*: Pale-yellow, plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, paraocular and interantennal areas, pronotal lobe, mesoscutum, scutellum, metanotum, ventral surface of front and mid trochanters, ventral margin of mid femur, S1; such hairs long on frontal and vertexal areas, mesepisternum, metepisternum, posteroventral ventral surface of front femur, ventral surface of hind trochanter; very long on upper margin of lateral

surface of propodeum. Genal area with off-white, plumose, erect, long hairs near proboscideal area (except for upper half with appressed hairs). Pale-yellow, erect, moderately short setae on dorsal surface of basitarsi and hind tibia; such hairs moderately long on mandible, posterior margin of basitarsi (except very long on hind basitarsus). Pale-yellow, suberect, short setae on dorsal surface of front and mid tibiae; thick setae on ventral surface of mid and hind tarsi (thickest towards distal margin). Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T1–T5 covered with pale-yellow, dense appressed hairs (except restricted to marginal zone of T5); T1 also with plumose, erect, long hairs; T2–T5 also with erect, minute setae (except moderately long on T4–T5 laterally). S2 with pale-yellow, erect, short hairs, which are branched only apically. Discs of S3–S5 with minute setae concentrated posteriorly; marginal zones with a line of plumose, moderately short hairs. S6 with short setae distributed mid-longitudinally and posteriorly.

*Surface sculpture:* Clypeal mid-longitudinal area with a mix of fine and moderately coarse punctures; punctation irregularly spaced ( $i=0.5-3d$ ); lateral area with very sparse punctures; lower 1/5 longitudinally striate; interspaces smooth. Malar area longitudinally striate on upper 2/3; substrigulate on lower 1/3. Supraclypeal area with a few moderately coarse punctures; interspaces imbricate. Paraocular area punctures crowded and moderately fine below (interspaces smooth); dense and fine above (interspaces rugulose). Frontal area densely and moderately finely punctate; interspaces rugulose. Vertexal area with minute punctures intermingled with moderately fine ones; interspaces rugose. Mesoscutum densely and moderately coarsely punctate (except coarsely and sparsely punctate mid-posteriorly); interspaces smooth. Scutellum and mesepisternum densely and coarsely punctate (except punctures crowded near scrobe); interspaces smooth. Metanotum punctures crowded and moderately fine. Metepisternum rugose above; obliquely striate medially; rugose below. Lateral surface of propodeum with very sparse fine punctures; interspaces imbricate. Upper area of vertical surface of metapostnotum smooth medially. Metasomal terga minutely punctate; interspaces smooth. Discs of S2–S5 sparsely and moderately finely punctate (except mid-longitudinal band impunctate); lateral area densely and finely punctate; interspaces imbricate. S6 densely and moderately finely punctate.

MALE (Figs. 36B, 36D, 36F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 8.5–9.7; head width 2.8–3.2; head length 2.3–2.5; intertegular distance 2.2–2.5; forewing length 7.1–7.8.

*Colouration*: F1 black. Dorsal surface of mediotarsi, wing veins pale-brown (except vein R of forewing black). Dorsal surface of tibiae and basitarsi, metasomal sterna dark-brown.

*Structure*: Clypeal mid-longitudinal area evenly deeply and narrowly (0.4x MOD) depressed on upper half. Malar area ~1.8x as long as basal depth of mandible (49:28). F1 slightly longer than its apical width (25:24). UID:LID (65:58). Horizontal surface of metapostnotum ~0.4x as long as metanotum (25:42); posterior transverse carina straight and interrupted medially. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~5x longer than broad (62:13). Outer rami of hind tarsal claws ~1.5x as long as inner rami (13:8). S7, S8 and genital capsule as in Figs. 37A, 37B, 37C, respectively.

*Pubescence*: Genal area with erect hairs only. Appressed hairs on T1–T3 restricted to marginal zones and lateral areas; on T4–T5 represented by a marginal line. Setae on S3–S6 evenly distributed.

*Surface sculpture*: Supraclypeal area rugose. Punctuation on frontal and vertexal areas difficult to discern from the rugulose integument. Mesoscutum moderately densely punctate (except sparsely punctate mid-posteriorly). Metanotum densely punctate. Mesepisternum moderately coarsely punctate; interspaces rugulose. T1–T2 finely punctate; T3–T6 with imbricate interspaces. Metasomal sterna densely and minutely punctate (except S2 sparsely punctate).

**Material studied:** *Primary type specimen*: Lectotype ♂ – “Dr. LENDL ADOLF; NEUQUEN 1907.”. “Colletes; longiceps; 1909 Friese det.”. “Type”. “Coll.; Friese”. “Zool. Mus.; Berlin”. “5”. “Zool. Mus.; Berlin”. “LECTOTYPE; Colletes longiceps; Friese, 1910; lab. Melo, 2015”. “<http://coll.mfn-berlin.de/u/; 58f9b7>”. {ZMB}.

*Additional specimens*: **ARGENTINA – Chubut**: 8km N of Sarmiento, (-45.512, -69.057), 264m, 26/xi/2003, [L.Packer], 3♀♀, {PCYU}. Loma del Medio, (-46.317, -70.735), 784m, 13/xi/2005, [A.Gravel], 2♀♀, {PCYU}. **Santa Cruz**: 0.5km E of Los Antiguos, (-46.558, -71.591), 232m, 21/xi/2003, [L.Packer], 1♀, {PCYU}. 23km W of Las Heras, (-46.613, -

69.639), 395m, 16/xi/2003, [L.Packer], 2♀♀2♂♂, {PCYU}. 43km E of Perito Moreno, (-46.434, -70.364), 534m, [L.Packer], 4♂♂, {PCYU}. **CHILE – Region XI:** Chile Chico, (-46.550, -71.716), 218m, 21/xi/1966, [Schlinger & Irwin], 1♂, {AMNH}.

**Range:** Argentina (Neuquén, Río Negro, Chubut, Santa Cruz), Chile (Region XI). See also Fig. 19A.

**Biogeographic distribution:** Andean region: Subantarctic sub-region (Valdivian Forest province); Patagonian sub-region (Patagonian province). Southern South American species distributed at altitudes of 200–800m a.s.l.

**DNA barcode:** Unavailable.

**Floral hosts:** Unknown.

**Comments:** Uncommon species restricted to southern South America. Even though almost all specimens of *C. longiceps* available to me have been collected in Argentina, the occurrence of the species in Chile was confirmed upon examination of the specimen from Chile Chico (Region XI) that Toro compared with the male lectotype (Toro 1999: 29). This small town is located at the north edge of the only semi-arid area in Patagonian Chile.



**Figure 37.** Dorsal view of the male terminalia of *C. longiceps*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

***Colletes lucens* Vachal, 1909**

(Figs. 38A–C)

*Colletes lucens* Vachal, 1909: 57; Toro 1986: 122; Moure & Urban 2002: 12; Moure *et al.* 2007: 683; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

Lectotype ♀ (examined). {MNHP}. [hereby designated]

*Colletes laticeps* Friese, 1910: 651; Claude-Joseph 1926: 134; Jaffuel & Pirion 1926: 364; Gazzula & Ruiz 1928: 300; Ruiz 1944: 201; Stephen 1954: 163; Roig-Alsina 1991: 259; Moure & Urban 2002: 11; Moure *et al.* 2007: 683. Synonymy proposed by Toro (1999: 29).

Lectotype ♀ (examined) designated by Moure & Urban (2002: 11). {ZMB}.

**Diagnosis:** The combination of malar area shorter than basal depth of mandible, mesoscutal pubescence pale-yellow, and marginal zones of T1–T5 covered with appressed hairs is sufficient to distinguish *C. lucens* from all *Colletes* species found in Chile, except *C. rutilans*, from which it can be differentiated by the pale-yellow mesoscutal pubescence (mesoscutal pubescence ferruginous in *C. rutilans*), and T1 inconspicuously punctate (T1 densely and moderately finely punctate in *C. rutilans*).

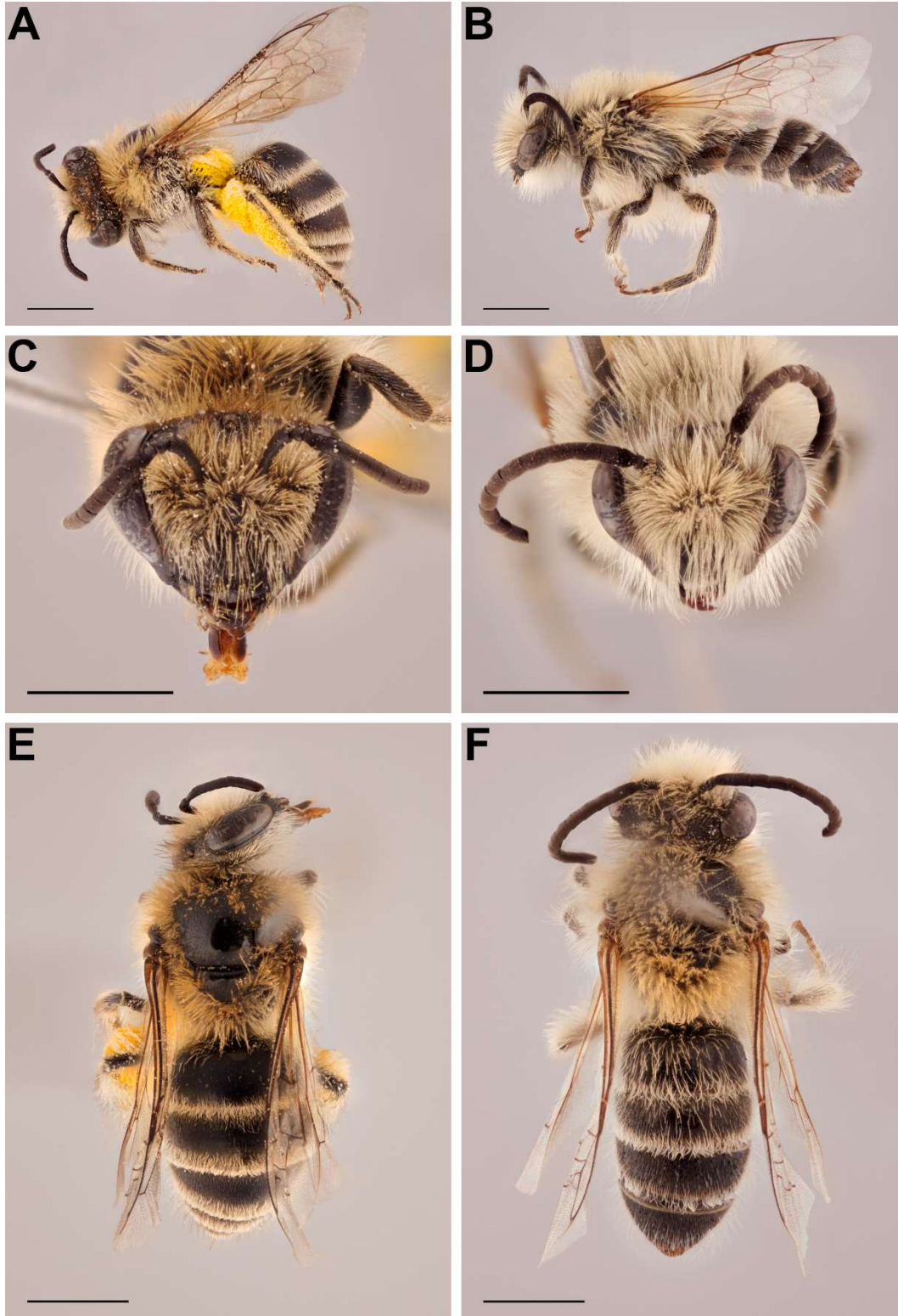
**Redescription:** FEMALE (Figs. 38A, 38C, 38E):

*Dimensions (mm):* Approximate body length 7.8–8.8; head width 2.7–2.9; head length 2.1–2.2; intertegular distance 1.9–2.1; forewing length 6.3–6.7.

*Colouration:* Black except pale-yellow on tibial spurs, proximal half of tarsal claws, marginal zones of T2–T5 and S2–S5. Reddish-brown on distal half of tarsal claws; marked on distal half of mandible. Dark-brown on tegula, vein R of forewing, anterior surface of mid femur, dorsal surface of mid and hind tibiae and tarsi (except distitarsi pale-brown). Pale-brown on wing veins, stigma, dorsal surface of distitarsi.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area neither depressed nor carinate; adjacent lateral area convex; apicomedial ridge absent. Malar area ~0.4x as long as basal depth of mandible (20:49). F1 ~1.3x as long as its apical width (31:24). UID:LID (65:61). Genal area concave behind upper summit of compound eyes in lateral view.





**Figure 38.** *Colletes lucens* Vachal, 1909. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum ~0.4x as long as metanotum (29:68); metapostnotal pits poorly-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa bearing a short spine (1.1x MOD). Posterior hind tibial spur ciliate. Hind basitarsus ~4x longer than broad (45:11). Outer rami of hind tarsal claws ~2.5x as long as inner rami (24:10). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Pale-yellow, plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, paraocular, frontal and genal (except moderately short behind eye) areas, pronotal lobe, mesoscutum, scutellum, posteroventral surface of front trochanter and femur, ventral surface of mid and hind coxa, ventral margin of mid femur, T1, S1–S2; such hairs long on interantennal and vertexal areas, mesepisternum, metepisternum, metanotum, upper margin of lateral surface of propodeum, ventral surface of hind trochanter. Pale-yellow, erect, moderately long setae on mandible, dorsal surface of tibiae (except suberect on front tibia) and tarsi; such hairs very long on posterior margin of mid and hind basitarsi. Bright-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. Pale-orange, suberect, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Discs of T2–T5 with bright-yellow, erect and suberect, short setae (moderately long on T4 and T5); marginal zones covered with pale-yellow appressed hairs. S3–S6 with pale-yellow, suberect, moderately short setae; longer and intermingled with plumose hairs on marginal zone.

*Surface sculpture:* Clypeus sparsely and moderately coarsely punctate on upper 2/3 (except slightly denser and finer on mid-longitudinal area); lower 1/3 longitudinally striate. Malar area with moderately fine punctures; interspaces substrigulate. Supraclypeal area imbricate but somewhat shiny. Paraocular area with moderately fine punctures; punctures crowded below; sparser above; interspaces smooth and shiny throughout. Frontal area densely and moderately coarsely punctate; interspaces rugulose and dull. Vertexal area with minute punctures intermingled with moderately fine ones; interspaces smooth; integument rugose near occipital area. Mesoscutum and scutellum sparsely and moderately finely punctate (except mesoscutal mid-posterior area largely impunctate and scutellar posterior 1/3 punctures crowded). Metanotum punctures crowded and moderately fine. Mesepisternum moderately coarsely and moderately densely punctate; interspaces smooth and shiny. Metepisternum smooth throughout. Lateral surface of propodeum impunctate, smooth and shiny. Upper area of vertical surface of

metapostnotum smooth medially. Punctuation on metasomal terga inconspicuous. S1–S4 finely and moderately densely punctate (except sparsely punctate on mid-longitudinal band); densely and moderately coarsely punctate on S5–S6; interspaces imbricate but shiny.

MALE (Figs. 38B, 38D, 38F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 7.3–7.9; head width 2.8–3.0; head length 2.1–2.2; intertegular distance 2.1–2.3; forewing length 6.8–7.1.

*Colouration*: Discs of metasomal sterna dark-brown. Marginal zone of S6 pale-yellow.

*Structure*: Malar area ~0.7x as long as basal depth of mandible (25:36). F1 ~0.9x as long as its apical width (26:30). UID:LID (67:51). Horizontal surface of metapostnotum ~0.5x as long as metanotum (19:37); metapostnotal pits well-delimited. Posteromedial surface of front coxa without spine. Hind basitarsus ~4.4x longer than broad (48:11). Outer rami of hind tarsal claws 2x as long as inner rami (20:10). Marginal zone S6 not depressed. S7, S8 and genital capsule as in Figs. 39A, 39B, 39C, respectively.

*Pubescence*: Pale-yellow hairs on paraocular area intermingled with black ones. Mesosomal pubescence longer throughout. Marginal zone of T5 without appressed hairs. Marginal zones of S3–S5 predominantly with plumose hairs.

*Surface sculpture*: Clypeal mid-longitudinal area punctures crowded. Supraclypeal area densely punctate (except impunctate on mid-longitudinal area). Upper area of metepisternum and lateral surface of propodeum rugose. Metasomal terga minutely punctate; sparsest on T1; successively denser towards T6.

**Material studied:** *Primary type specimens*: Lectotype ♀ of *C. lucens* – “CHILE; CONCEPC.; 2.1905; P. HERBST”. “Colletes ♀; lucens; Vach.” “MUSEUM PARIS; COLL. J. VACHAL 1911”. “LECTOTYPE”. “LECTOTYPE; Colletes lucens ♀; Vachal, 1909; designated R. Ferrari, 2017”. {MNHP}. [hereby designated]. Lectotype ♀ of *C. laticeps* – “CHILE; CONCEPC.; II 1904; P. HERBST”. “Colletes; laticeps; 1909 Friese det.”. “Type”. “LECTOTYPE; Colletes laticeps; Friese, 1910; lab. Melo, 2015”. “<http://coll.mfn-berlin.de/u/; 58f9b8>”. “Zool. Mus.; Berlin”. {ZMB}.

*Secondary type specimen:* Paralectotype ♂ of *C. lucens* – **CHILE** – **Region VIII:** Concepción, ii/1905, 1♂, {MNHP}.

*Additional specimens:* **CHILE** – **Region IV:** Panamericana Road km 232.5, (-31.851, -71.514), 75m, 2/ii/2016, [L.Packer], 1♂, {PCYU}. Road 5 km 232, 27/ii/2006, [L.Compagnucci], 1♂, {MACN}. Fray Jorge National Park, (-30.644, -71.657), 211m, 12/xi/2003, [F.Parker], 1♂, {BBSL}. **Region Metropolitana:** Quilicura, (-33.347, -70.729), 472m, x/1979, [L.Peña], 1♂, {AMNH}. **Region VI:** La Correana, 21/ii/1977, [L.Peña], 2♀♀, {AMNH}; idem, except 16/ii/1977, 2♀♀. Rancagua, (-34.187, -70.768), 505m, 1906, [E.Reed], 1♀, {BBSL}. **Region VII:** Curicó, (-34.985, -71.258), 203m, 20/ii/1960, [L.Peña], 1♂, {AMNH}. Highway 115 to Laguna del Maule, 4/i/2009, [L.Packer], 2♂♂, {PCYU}. Laguna del Teno, (-35.164, -70.530), 2695m, 26/i/2016, [L.Packer], 1♀, {PCYU}. Linares, (-35.847, -71.606), 158m, 9/ii/1976, [H.Toro], 1♀, {PUCV}. **Region VIII:** E of Antuco, (-37.345, -71.549), 715m, 3/iii/2013, [Postlethwaite & Monckton], 1♀, {PCYU}. Lanalhue, (-37.909, -73.378), 47m, 19/i/1984, [S.Gutierrez], 1♂, {PUCV}. Las Trancas, (-36.913, -71.500), 1225m, 17/i/1953, [L.Peña], 1♂, {KUNHM}; idem, except i/1987, 4♂♂, {AMNH}. **Region IX:** Angol, (-36.834, -73.047), 82m, iii/1986, [L.Peña], 1♂, {AMNH}. Loncoche, (-39.369, -72.639), 112m, i/1986, [L.Peña], 2♂♂, {AMNH}. Lonquimay, (-38.725, -72.601), 111m, xii/1979, [L.Peña], 1♂, {AMNH}. Maite Bajo, (-39.333, -71.503), 495m, 29/i/2016, [L.Packer], 1♀, {PCYU}.

**Range:** Chile (Regions IV–X). See also Fig. 30C.



**Figure 39.** Dorsal view of the male terminalia of *C. lucens*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Biogeographic distribution:** Andean region: Central Chilean sub-region (Coquimban and Santiagan provinces). Subantarctic sub-region (Maule province). Central Chilean species distributed at altitudes of 0–2700m a.s.l.

**DNA barcode:** Available. BOLD: ADC8390 (1♀2♂♂). Distance from the nearest neighbour (*C. flavipilosus* n. sp.): 4.7–5.59%.

**Floral hosts:** Apiaceae – *Eryngium paniculatum* Cav. & Dombey ex F. Delaroché (this study). Compositae – *Baccharis* sp. (Fries 1910, Toro 1999); *Senecio rutaceus* Phil. (Jaffuel & Pirion 1926).

**Comments:** Uncommon species distributed in central Chile.

Examination of the lectotypes of *C. lucens* and *C. laticeps* confirmed that the latter is a junior synonym of the former, as originally proposed by Toro (1999: 29). This synonymy has been acknowledged also by Ascher & Pickering (2017), but not by Moure & Urban (2002) and Moure *et al.* (2007). The vast majority of the available information on *C. lucens* in the literature has originally been attributed to *C. laticeps* (refer to the synonymy, above).

### ***Colletes mastochila* Moure, 1956**

(Figs. 40A–F)

*Colletes mastochila* Moure, 1956: 206; Toro 1986: 122, 1999: 29; Moure & Toro 2002: 13; Moure *et al.* 2007: 683; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

Holotype ♀ (examined). {DZUP}.

**Diagnosis:** The following combination of characteristics differentiates *C. mastochila* from all other Chilean species of the genus: labral median area swollen, female clypeal lower 1/5 with mid-longitudinal ridge, mesoscutal pubescence with off-white and black hairs intermixed, and discs of T2–T4 without appressed hairs.





**Figure 40.** *Colletes mastochila* Moure, 1956. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.



*Colletes mastochila* is most similar to *C. nigropilosus* **n. sp.**, from which it can be distinguished by the lateral surface of propodeum with imbricate interspaces (lateral surface of propodeum with smooth interspaces in *C. nigropilosus* **n. sp.**); and T1 covered with off-white hairs (T1 pubescence mostly black in *C. nigropilosus* **n. sp.**). *Colletes mastochila* can also be confused with *C. alocochila*, however, the former is considerably longer, about 12.0/11.5 mm (♀/♂) in length (*C. alocochila* is about 9.5/9.0 mm in length); and has the lateral surface of propodeum with imbricate interspaces (lateral surface of propodeum with smooth interspaces in *C. alocochila*).

**Redescription:** FEMALE (Figs. 40A, 40C, 40E):

*Dimensions (mm):* Approximate body length 11.5–12.3; head width 3.5–3.7; head length 2.6–2.7; intertegular distance 2.9–3.1; forewing length 7.8–8.3.

*Colouration:* Black except reddish-brown on distal half of tarsal claws; marked on distal half of mandible. Dark-brown on tegula, wing veins (except basal veins of forewing black), front coxa, anteroventral surface of mid trochanter and femur, tibial spurs, medio and distitarsi, marginal zones of T1–T4, ventrally reflexed lateral areas of T1–T2, S1, lateral area of S2. Pale-brown on proximal half of tarsal claws.

*Structure:* Labrum medially convex; convexity not margined by ridges. Clypeal mid-longitudinal area evenly narrowly (0.3x MOD) and shallowly depressed on upper 4/5; adjacent lateral area convex; apicomedial ridge present. Malar area 1.25x as long as basal depth of mandible (30:24). F1 ~1.3x as long as its apical width (40:30). UID:LID (77:75). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.35x as long as metanotum (24:66); propodeal pits well-delimited; posterior transverse carina sinuous and narrowly interrupted medially. Posteromedial surface of front coxa bearing long spine (0.6x MOD). Posterior hind tibial spur pectinate. Hind basitarsus ~3x longer than broad (56:19). Outer rami of hind tarsal claws ~2.2x as long as inner rami (26:12). Posterolateral area of S6 convex but lacking carina; marginal zone depressed.

*Pubescence:* Black, long, plumose on lateral slopes of clypeus and supraclypeal area, paraocular area, genal and frontal areas, scutellum, mesepisternum, metepisternum; very long on vertexal area, metanotum, upper margin of lateral surface of propodeum. Mixed off white and

black, plumose, moderately short on interantennal area, pronotal lobe, mesoscutum. Black, erect, moderately long setae on mandible, posterior surface of front tibia and basitarsi, anterior surface of mid tibia, dorsal surface of mid and hind basitarsi, hind tibia (except anterior surface), lateral areas of T2–T5, S1–S2, posterior 1/3 of S3–S5, mid-longitudinal area of S6; such hairs long on posterior margin of mid basitarsus and tarsomere 2, posterolateral areas of T3–T5; very long on posterior margin of hind basitarsus and tarsomere 2. Black, suberect, moderately short setae on dorsal surface of front and mid tibiae; such setae thick on ventral surface of mid and hind tarsi (thickest towards distal margin). Lower area of lateral surface of propodeum with off-white appressed hairs. T1 with off-white, plumose, long hairs.

*Surface sculpture:* Clypeal mid-longitudinal depression with fine punctures; convex area adjacently to depression and lower 1/3 longitudinally striate. Supraclypeal area impunctate and imbricate (except smooth upper 1/5). Malar area substrigulate on lower margin; costulate elsewhere. Paraocular area coarsely and densely punctate below; punctures crowded above. Vertexal area sparsely shallowly punctate interspaces smooth); integument rugose near ocellus. Mesoscutal anterior and lateral areas moderately coarsely and densely punctate; slightly denser and coarser on posterior margin; disc sparsely punctate. Scutellum densely punctate; coarsely punctate on disc; progressively finer towards posterior margin. Metanotal punctation difficult to discern from the overall rugose integument. Mesepisternum densely and moderately coarsely punctate anteriorly; very densely and moderately finely punctate posteriorly. Metepisternum obliquely striate medially; rugulose above and below. Lateral surface of propodeum sparsely finely punctate; interspaces imbricate. Upper area of vertical surface of metapostnotum rugose medially. Metasomal terga minutely and shallowly punctate; sparsest on T1, densest on T2–T3; interspaces smooth and shiny. Metasomal sterna finely and moderately densely punctate (except impunctate on anterior 1/3 of S3–S4 and S6); coarser on mid-longitudinal area of S6; interspaces imbricate throughout but somewhat shiny.

MALE (Figs. 40B, 40D, 40F). As in female, except for usual secondary sexual characteristics and as follows:

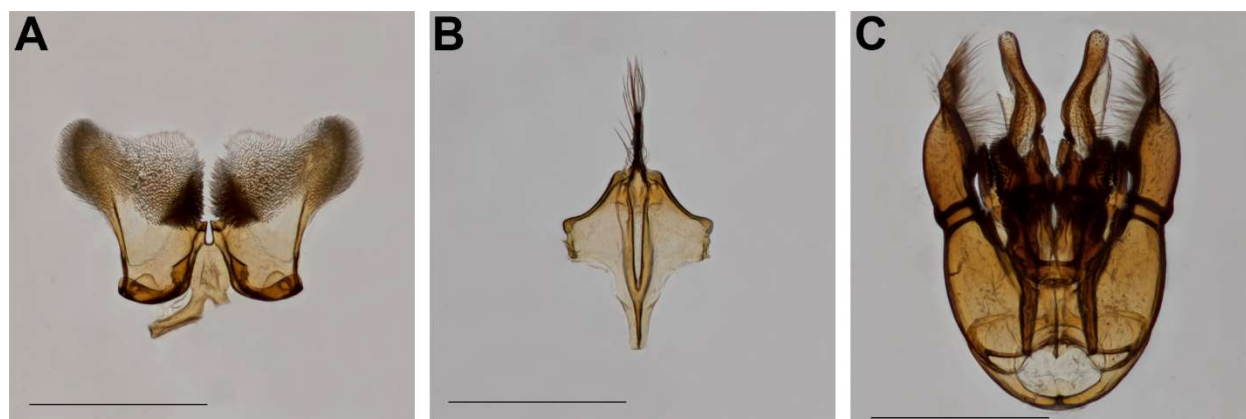
*Dimensions (mm):* Approximate body length 10.7–11.5; head width 3.3–3.6; head length 2.6–2.8; intertegular distance 2.4–2.7; forewing length 7.9–8.5.

*Colouration:* Dark-brown on stigma, anteroventral surface of front trochanter and femur, dorsal surface of mid trochanter, anterior surface of mid and hind tibiae, basitarsi, proximal half of S2–S5, proximal and distal 1/3 of S6. Marginal zones of T1–T4, wing veins (except vein R of forewing black) pale-brown.

*Structure:* Clypeal mid-longitudinal depression broader ( $\sim 0.5\times$  MOD); apicomedial ridge absent. Malar area  $\sim 1.7\times$  as long as basal depth of mandible (40:24). F1  $\sim 1.3\times$  as long as its apical width (36:28). UID:LID (79:72). Horizontal surface of metapostnotum nearly half as long as metanotum (26:70). Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 3.5\times$  longer than broad (71:21). Outer rami of hind tarsal claws  $\sim 1.3\times$  as long as inner rami (18:14). Posterolateral area of S6 flat; marginal zone not depressed. S7, S8 and genital capsule as in Figs. 41A, 41B, 41C, respectively.

*Pubescence:* Off-white, very long on lateral slopes of clypeus. Very long on mesoscutum, T1. Lower area of lateral surface of propodeum with black, long hairs. Short, plumose, suberect on marginal zones of S2–S4.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and finely punctate; adjacent convex area lacking sulci. Supraclypeal area with very sparse moderately coarse punctures; interspaces smooth and shiny. Vertexal area moderately finely punctate. Mesoscutal anterior half coarsely and very densely punctate. Lateral surface of propodeum rugose posteriorly. Upper area of vertical surface of metapostnotum transversely striate medially. Metasomal terga finely punctate. Metasomal sterna finely and densely punctate throughout.



**Figure 41.** Dorsal view of the male terminalia of *C. mastochila*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** *Primary type specimen:* Holotype ♀ – “PUTRE, Arica; II-1948; Pe. G. Kuschel”. “HOLOTIPO”. “mastochilus”. {DZUP}.

*Secondary type specimens:* Paratypes ♀♀ and ♂: **CHILE** – **Region XV:** Putre, ii/1948, [G.Kuschel], 3♀♀, {DZUP}; idem, except 1♀, {KUNHM}; idem, except 1♀, {AMNH}. **PERU** – **Tacna:** Rio Sama, xii/1940, [P.S], 1♂, {DZUP}.

*Additional specimens:* **ARGENTINA** – **Salta:** Valle Encantado, 9/i/1994, [C.Schindwein], 2♂♂, {UFMG}; idem, except 1♂, {DZUP}; idem, except 12/i/1994, 1♀, {DZUP}; idem, except 14/i/1994, 1♂, {DZUP}; idem, except 15/i/1994, 1♀; idem, except 15/i/1994, 1♀, {DZUP}. **Catamarca:** 8km S of Chapillitas, (-27.385, -66.385), 3130m, 15/ii/2003, [L.Packer], 1♀, {PCYU}. **BOLIVIA** – **La Paz:** Achacachi, (-16.044, -68.678), 3858m, 11/xii/1948, [G.Kuschel], 2♀♀, {DZUP}. **CHILE** – **Region XV:** Putre, (-18.194, -69.561), 3530m, 18/ii/1984, [M.Arroyo], 2♂♂, {KUNHM}; idem, except 30/xi/1970, [H.Toro], 1♀, {AMNH}. **Region II:** Puquios, (-20.999, -68.387), 4178m, 8/i/1971, [L.Ruz], 1♀, {AMNH}.

**Range:** Argentina (Salta, Catamarca), Bolivia (La Paz), Chile (Regions XV, I, II), Peru (Tacna). See also Fig. 30C.

**Biogeographic distribution:** South American transition zone: Desert, Puna, Atacama and Monte provinces. Western South American species distributed at altitudes of 3100–4200m a.s.l.

**DNA barcode:** Available. BOLD: ABW4685 (1♀). Distance from the nearest neighbour (*C. cognatus*): 5.98–6.91%.

**Floral hosts:** Loasaceae – *Caiophora cirsiifolia* C. Presl (this study).

**Comments:** *Colletes mastochila* is a rare species only found at very high altitudes (3000m a.s.l. or higher). The species is also distributed in northwestern Argentina, western Bolivia and southern Peru.

Despite considerable fieldwork in the far north of Chile over the last 30 years – including localities where the species is known to occur – Packer and colleagues have collected no

specimen of *C. mastochila* in the country. Although pan traps have proved to be remarkably effective at capturing a series of *Colletes* species in northern Chile, no *C. mastochila* has ever been trapped. Perhaps, traps are not attractive to *C. mastochila*, and the species is specialist in flowers of the genus *Caiophora* (Loasaceae).

The holotype of *C. mastochila* is a female, not a male, as reported by Moure *et al.* (2007). This error, however, seem to have been simply typographical in the original description (Moure 1956: 208).

### ***Colletes murinus* Friese, 1900**

(Figs. 42A–F)

*Colletes murinus* Friese, 1900: 184; Toro 1986: 122; Moure & Urban 2002: 14; Moure *et al.* 2007: 684; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

Lectotype ♀ (examined) designated by Moure & Urban (2002: 14). {ZMB}.

**Diagnosis:** The combination of clypeal mid-longitudinal area depressed and lacking carina, mesosomal pubescence with off-white and black hairs intermixed, and T2–T5 black and covered with pale-yellow appressed hairs is sufficient to differentiate *C. murinus* from all other Chilean species of the genus, except *C. ventricarinatus* **n. sp.** The female of these species, however, can be distinguished by clypeus with a pair of pits subapically in *C. murinus* (clypeus with a transverse depression subapically in *C. ventricarinatus* **n. sp.**); and S6 not carinate laterally in *C. murinus* (S6 carinate laterally in *C. ventricarinatus* **n. sp.**). The males can be differentiated by F2 1.4x as long as F1 in *C. murinus* (F2 1.2x as long as F1 in *C. ventricarinatus* **n. sp.**); and mesepisternal interspaces smooth in *C. murinus* (mesepisternal interspaces rugulose in *C. ventricarinatus* **n. sp.**).

**Redescription:** FEMALE (Figs. 42A, 42C, 42E):

*Dimensions (mm):* Approximate body length 8.5–9.6; head width 3.3–3.7; head length 2.5–2.8; intertegular distance 2.7–3.0; forewing length 7.8–8.6.

*Colouration:* Black except dark-brown on tegula, wing veins (except vein R of forewing), stigma, ventrally reflexed lateral areas of T1–T2, marginal zones of T1–T4. Reddish-brown on

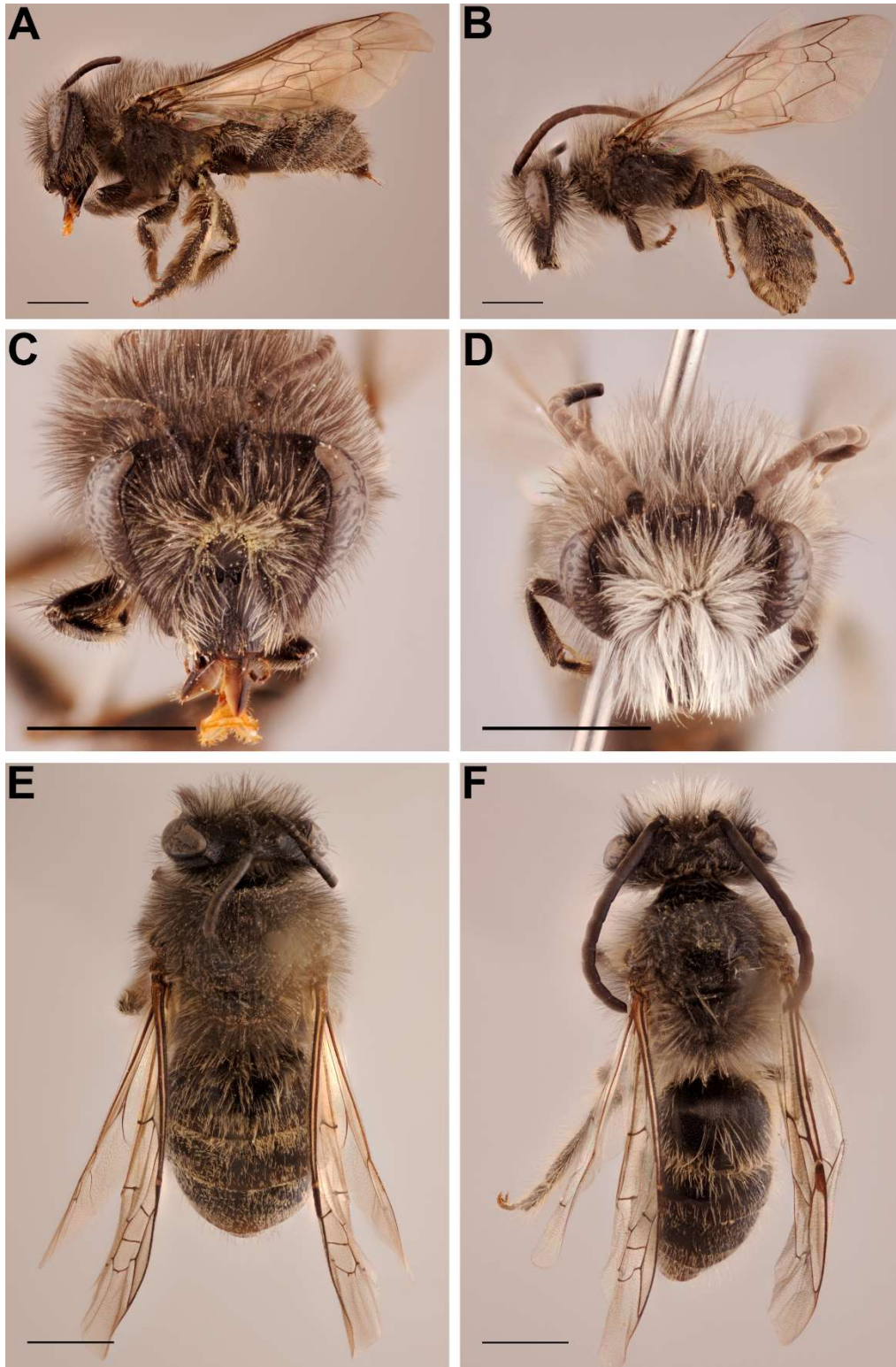
distal half of tarsal claws; marked on distal half of mandible. Pale-brown on tibial spurs, distitarsi, proximal half of tarsal claws, marginal zones of S1–S5.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area evenly deeply depressed; depression narrow (0.4x MOD) on upper 1/3, broader (=MOD) on middle 1/3; adjacent lateral area convex; apicomedial ridge absent. Malar area ~1.6x as long as basal depth of mandible (38:28). F1 ~1.4x as long as its apical width (30:21).

UID:LID (72:68). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum ~0.3x as long as metanotum (14:40); metapostnotal pits well-delimited; posterior transverse carina straight and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.6x longer than broad (50:14). Outer rami of hind tarsal claws ~2.3x as long as inner rami (28:12). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Mixed off-white and black hairs, plumose, erect, long on paraocular and interantennal areas, genal area (ranging from moderately short behind upper summit of eye to very long near proboscival fossa), metanotum; moderately long on lateral slopes of clypeus and supraclypeal area, pronotal lobe, mesoscutum, scutellum; with only black hairs on frontal and vertexal areas, mesepisternum, metepisternum, upper margin of lateral surface of propodeum (except very long), ventral surface of coxae and front and mid trochanters (except moderately short), posteroventral surface of front trochanter and femur. Black, erect, moderately long setae on mandible, dorsal surface of mid and hind tibiae and basitarsi; such hairs long on posterior surface of front tibia, posterior margin of front basitarsus, distal half of posterior surface of hind tibia; very long on posterior margin of mid and hind basitarsi. Fulvous, suberect, moderately short, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Black, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T1–T5 covered with pale-yellow dense appressed hairs (slightly sparser on T1); T1 also with pale-yellow, plumose, erect, long hairs; short on T2–T3; T4–T5 with black, moderately long setae. S1 with fulvous, plumose, erect, moderately long hairs. S2 with black, erect, short hairs, which are branched only apically. S3–S6 with fulvous, erect, moderately short setae.





**Figure 42.** *Colletes murinus* Friese, 1900. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and finely punctate; adjacent convex area with very sparse fine punctures; integument longitudinally striate near apicolateral corner; interspaces smooth throughout. Malar area minutely punctate near eye; longitudinally striate elsewhere. Supraclypeal upper half smooth; lower half imbricate. Paraocular area densely and moderately finely punctate throughout (except slightly sparser and coarser towards antennal socket); interspaces smooth and shiny. Frontal area densely and moderately coarsely punctate; interspaces rugulose but somewhat shiny. Vertexal area with moderately coarse punctures intermingled with fine ones; densely punctate on half near lateral ocellus; sparsely punctate on half near eye. Dorsal mesosoma with smooth and shiny interspaces throughout. Mesoscutum moderately finely and moderately densely punctate (except sparsely punctation mid-posterior area). Scutellum and metanotum densely and moderately coarsely punctate (except slightly finer on latter). Mesepisternum moderately sparsely and moderately finely punctate; interspaces smooth (except rugulose anteriorly episternal groove). Metepisternum rugose above; obliquely striate medially; smooth below. Lateral surface of propodeum finely and moderately densely punctate; interspaces rugulose. Upper area vertical surface of metapostnotum transversely striate medially. Metasomal terga minutely and moderately densely punctate (except T1 sparsely punctate); interspaces smooth and shiny. Metasomal sterna minutely and sparsely punctate (except posterior half of S6 densely and moderately finely punctate); interspaces imbricate.

MALE (Figs. 42B, 42D, 42F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 7.4–8.1; head width 3.1–3.2; head length 2.3–2.4; intertegular distance 2.0–2.2; forewing length 6.9–7.3.

*Colouration:* Middle 1/3 of mandible black. Wing veins pale-browns (except veins R and C of forewing dark-brown). Proximal half of distitarsi dark-brown.

*Structure:* Labrum medially concave; concavity not margined by lateral ridges. Clypeal mid-longitudinal area evenly shallowly depressed; depression narrow (0.5x MOD) on upper 1/3; broader (0.8x MOD) on middle 1/3. Malar area ~2.3x as long as basal depth of mandible (56:24). F1 about as long as its apical width (28:27). UID:LID (72:60). Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum ~0.5x as long as metanotum (24:46).

Hind basitarsus ~4x longer than broad (49:12). Outer rami of hind tarsal claws ~1.7x as long as inner rami (28:16). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 43A, 43B, 43C, respectively.

*Pubescence*: Off-white on lateral slopes of clypeus, supraclypeal area, legs (except front tibia with a few black hairs). Marginal zones of S1–S5 with a band of off-white, plumose, suberect, short hairs.

*Surface sculpture*: Clypeal striae restricted to lower 1/5. Supraclypeal area moderately densely punctate. Malar lower 1/4 smooth. Frontal area punctures crowded. Metanotal interspaces imbricate. Upper area vertical surface of metapostnotum rugulose medially. Metasomal terga finely punctate; T1 moderately densely punctate. S6 evenly finely punctate.

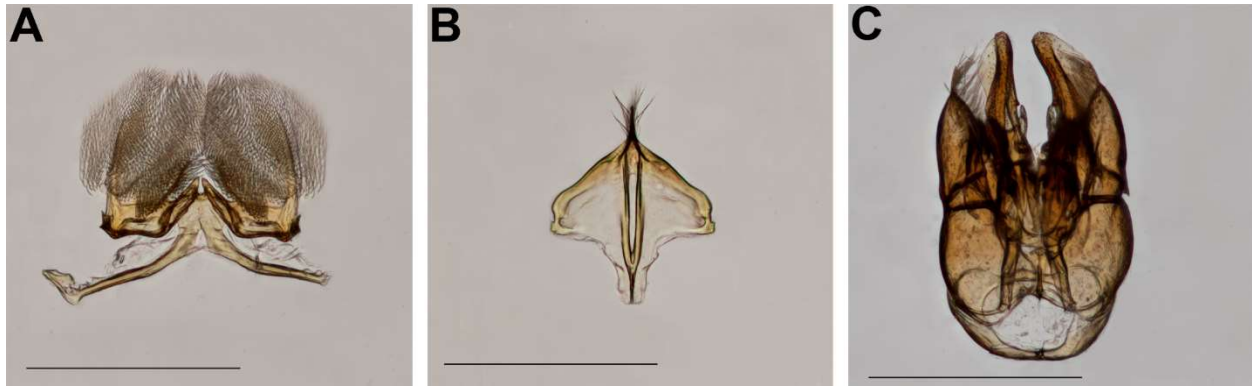
**Material studied:** *Primary type specimen*: Lectotype ♀ – “Peru; Callanga; 98”. “Colletes ♀; murinus; 1900 Friese det.”. “Type”. “Coll.; Friese”. “Zool. Mus.; Berlin”. “LECTOTYPE; Colletes murinus; Friese, 1900; lab. Melo, 2015”. “<http://coll.mfn-berlin.de/u/;58f9c1>”. {ZMB}.

*Additional specimens*: **CHILE – Region XV**: NE of Putre, (-18.180, -69.524), 4040m, 2/xi/2013, [S.Monckton], 1♂, {PCYU}. Pucará Belén, (-18.472, -69.527), 3178m, 1/xi/2013, [S.Monckton], 1♂, {PCYU}. **Region I**: Mamiña, (-20.062, -69.222), 2757m, 30/i/1972, [Montenegro], 1♀, {PCYU}. **Region II**: Calama, (-22.466, -68.897), 2317m, ii/1992, [L.Peña], 1♂, {AMNH}. Chiu-Chiu, (-22.337, -68.615), 2555m, 30/iii/2000, [L.Packer], 4♂♂, {PCYU}. Road to Matancilla, (-22.665, -68.230), 3079m, 21/xi/2013, [Postlethwaite & Monckton], 1♀1♂, {PCYU}. San Pedro de Atacama, (-22.910, -68.211), 2422m, 7/i/1971, [H.Toro], 1♂, {PUCV}; idem, except [L.Ruz], 1♂, {AMNH}. Toconao, (-23.193, -67.998), 2519m, 9/xii/1996, [U.Peña], 1♀, {AMNH}.

**Range**: Chile (Regions XV, I, II), Peru (Lima). See also Fig. 30B.

**Biogeographic distribution**: South American transition zone: Desert and Atacama provinces. Northern Chilean and Southern Peruvian species distributed in the summer rainfall area at altitudes of 2300–4100m a.s.l.

**DNA barcode**: Unavailable.



**Figure 43.** Dorsal view of the male terminalia of *C. murinus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Floral hosts:** Unknown.

**Comments:** Uncommon species originally described from Peru, and its occurrence in Chile was reported only very recently (Ascher & Pickering 2017). This probably explains the reason why Toro (1999) did not include this species in his key for the Chilean *Colletes*, although I have studied one male *C. murinus* that Toro caught himself in San Pedro de Atacama (Region II) in 1971. The remarkable morphological homogeneity that the male *C. murinus* shares with males of other species (e.g. *C. gilvus*, *C. ventricarinatus* n. sp., *C. alocochila*) probably prevented Toro from assessing the actual identity of that male specimen.

### ***Colletes musculus* Friese, 1910**

(Figs. 44A–F)

*Colletes musculus* Friese, 1910: 647, 1912: 366; Stephen 1954: 163; Toro 1986: 123, 1999: 29; Moure & Urban 2002: 15; Moure *et al.* 2007: 684; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

Lectotype ♀ (examined) designated by Moure & Urban (2002: 15). {ZMB}.

*Colletes ciliatus* Friese, 1910: 647 (junior homonym of *Colletes ciliatus* Patton, 1879: 369); Claude-Joseph 1926: 136; Jaffuel & Pirion 1926: 364; Ruiz 1944: 209; Stephen 1954: 161; Toro & Cabezas 1977: 53.

Lectotype ♀ (examined) designated by Toro & Cabezas (1977: 53). {ZMB}.

*Colletes biciliatus* Cockerell, 1918a: 138 [new name for *Colletes ciliatus* Friese (not Patton)]; Moure *et al.* 2007: 678. Synonymy proposed by Toro (1999: 29).

*Colletes chubutensis* Cockerell, 1918a: 137; Pérez & Cerda 1980: 100; Moure & Urban 2002: 6; Moure *et al.* 2007: 680. Synonymy proposed by Toro (1999: 29).

Lectotype ♂ (examined). {USNM}. [hereby designated]

*Colletes polynidus* Stephen, 1953: 40 [unnecessary new name for *Colletes ciliatus* Friese (not Patton)].

*Mourecotelles biciliatus*; Moure & Urban 2002: 23; Montalva & Ruz 2010: 23.

**Diagnosis:** *Colletes musculus* can be differentiated from the other species of the genus found in Chile through the following combination of characteristics: head and mesosoma covered with off-white and black hairs intermixed, mesosomal interspaces imbricate throughout, and T1–T5 dark-blue with dark-brown marginal zones.

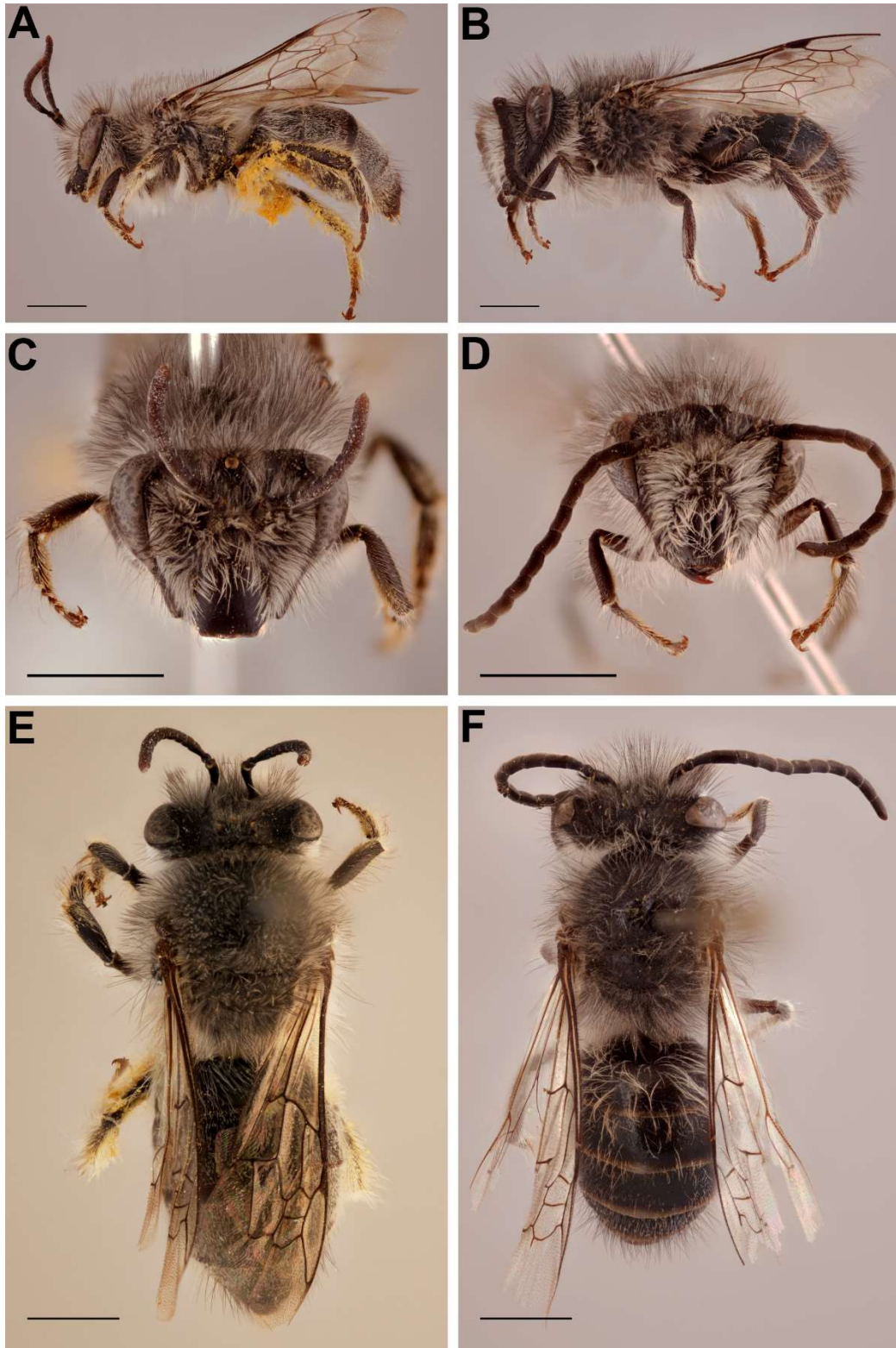
*Colletes musculus* is most similar to *C. cyanescens*, from which it is distinct in having opaque dark-blue T1–T5 (T1–T5 metallic greenish-blue in *C. cyanescens*); and marginal zones of T1–T4 dark-brown, contrasting with the colour of discs (marginal zones of T1–T4 the same colour as discs, in *C. cyanescens*).

**Redescription:** FEMALE (Figs. 44A, 44C, 44E):

*Dimensions (mm):* Approximate body length 8.2–9.8; head width 3.2–3.6; head length 2.5–2.8; intertegular distance 2.5–2.9; forewing length 7.4–7.9.

*Colouration:* Black except opaque dark-blue on T1–T5. Dark-brown on tegula, wing veins (except veins C and R of forewing black), mid trochanter and femur, anterior surface of mid tibia, hind coxa and trochanter, dorsal surface of tarsomeres 2–5 (except pale-brown on distal 1/5 of distitarsi), marginal zones of T1–T4, ventrally reflexed lateral areas of T1, S6 laterally. Reddish-brown marked on distal half of mandible. Pale-brown on tibial spurs, distal half of tarsal claws, mid-longitudinal band of S6. Pale-yellow on proximal half of tarsal claws, marginal zones of S1–S5.





**Figure 44.** *Colletes musculus* Friese, 1910. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.



*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area evenly shallowly and narrowly (0.4x MOD) depressed on upper 3/5; adjacent lateral area convex; apicomedial ridge absent. Malar area ~1.4x as long as basal depth of mandible (31:22). F1 ~1.6x as long as its apical width (34:21). UID:LID (70:71). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded. Horizontal surface of metapostnotum ~0.3x as long as metanotum (18:58); metapostnotal pits well-delimited; posterior transverse carina straight and virtually complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~4x longer than broad (53:13). Outer rami of hind tarsal claws 1.8x as long as inner rami (15:7). Posterolateral area of S6 flat and lacking carina; marginal zone not depressed.

*Pubescence:* Mixed off-white and black, plumose, erect, moderately long on lateral slopes of supraclypeal area, paraocular area, genal area (except very long towards proboscoid fossa and black hairs restricted to outer margin of eye), pronotal lobe, mesoscutum, scutellum, anteroventral surface of front trochanter and femur, ventral surface of mid trochanter; long on interantennal and frontal areas, mesepisternum, metepisternum; such hairs very long on vertexal area, upper margin of lateral surface of propodeum. Off-white, plumose, suberect, moderately short on clypeal mid-longitudinal and vertical areas; erect, long on ventral margin of mid femur, T1, S1. Pale-yellow, erect, moderately short setae on mandible, dorsal surface of mid and hind basitarsi and hind tibia. Black, plumose, erect, long on posterior margin of front and mid basitarsi; such hairs very long on posterior margin of hind basitarsus. Pale-yellow, suberect, short setae on dorsal surface of front and mid; setae thick on ventral surface of mid and hind tarsi (thickest towards distal margin). Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T2–T5 covered with off-white, sparse appressed hairs; T2 also with off-white, plumose, moderately long hairs; T3–T5 also with black, erect, moderately short setae (except pale-yellow, short on T3). Discs of S2–S5 with suberect, minute setae; marginal zones with a line of plumose, erect, short hairs. S6 with fulvous, erect, short setae concentrated laterally and posteriorly.

*Surface sculpture:* Clypeal mid-longitudinally depression sparsely and moderately finely punctate (interspaces longitudinally striate); adjacent convex area densely punctate on lateral slopes (interspaces imbricate). Malar area substrigulate. Supraclypeal area with a few moderately fine punctures; interspaces imbricate. Paraocular area densely and moderately finely punctate

below; sparsely and finely punctate above; interspaces imbricate throughout. Punctuation on frontal area difficult to discern from the overall rugose interspaces. Vertexal area finely and moderately sparsely punctate (interspaces imbricate); integument rugose near eye and occipital area. Mesoscutum moderately finely and moderately densely punctate (except sparsely punctate on mid-posterior area); interspaces imbricate. Scutellum moderately coarsely and moderately densely punctate (except sparsely punctate anteriorly); interspaces imbricate (except rugose on posterior 1/5). Punctures on metanotum very ill-defined, punctures limits somehow rugose. Mesepisternum sparsely and moderately finely punctate. Metepisternum imbricate above and below; rugose medially. Upper area of vertical surface of metapostnotum rugose. Metanotal terga minutely punctate; interspaces imbricate throughout. Metasomal interspaces imbricate. S2–S5 finely and sparsely punctate (except moderately densely punctate posterolaterally). S6 moderately finely punctate (except minutely punctate mid-longitudinally).

MALE (Figs. 44B, 44D, 44F). As in female, except for usual secondary sexual characteristics and as follows:

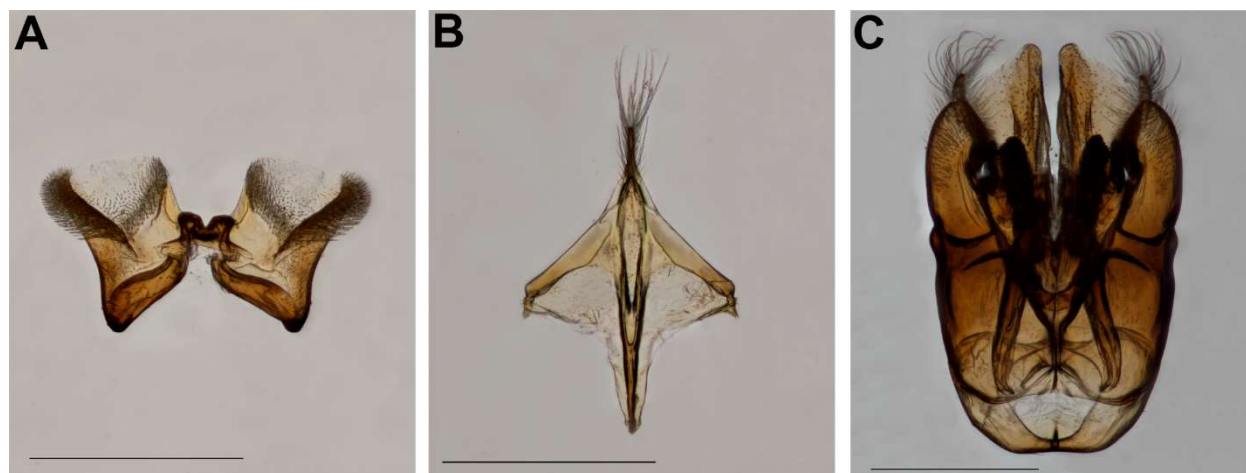
*Dimensions (mm)*: Approximate body length 8.0–9.1; head width 3.3–3.7; head length 2.6–3.0; intertegular distance 2.5–2.9; forewing length 7.2–7.9.

*Colouration*: Reddish-brown mark on mandible restricted to distal 1/3. Legs black, except dark-brown on dorsal surface of distitarsi. Tibial spurs pale-yellow. S6 dark-brown entirely.

*Structure*: Labrum medially convex; convexity not margined by ridges. Clypeal mid-longitudinal area deeply and narrowly (0.5x MOD) depressed on upper half; depression shallow and broad (2x MOD) below. Malar area ~2x as long as basal depth of mandible (35:17). F1 ~1.1x as long as its apical width (33:29). UID:LID (79:73). Horizontal surface of metapostnotum 0.4x as long as metanotum (18:45); metapostnotal pits well-delimited; posterior transverse carina sinuous and interrupted medially. Hind basitarsus ~3.2x longer than broad (42:13). Outer rami of hind tarsal claws 1.5x as long as inner rami (15:10). S7, S8 and genital capsule as in Figs. 45A, 45B, 45C, respectively.

*Pubescence*: Hairs on clypeal lateral slopes as long as those on paraocular area. Front and mid basitarsi with pale-yellow setae. S2 without appressed hairs; on S3 restricted laterally. Setae on S3–S5 evenly distributed on discs.

*Surface sculpture:* Clypeal mid-longitudinal depression with smooth interspaces. Vertexal area punctures crowded near ocellus. Scutellar posterior 1/5 with imbricate interspaces. Punctuation on discs of S2–S5 evenly distributed. S6 finely punctate throughout.



**Figure 45.** Dorsal view of the male terminalia of *C. musculus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** *Primary type specimens:* Lectotype ♀ of *C. musculus* – “Dr. LENDL ADOLF; NEUQUEN 1907.”. “Colletes; musculus; 1909 Friese det.”. “SYNTYPE; Colletes; musculus Fr.; Examined C Rasmussen’ 07”. “LECTOTYPE; Colletes musculus; Friese, 1910; lab. Melo, 2015”. “Zool. Mus.; Berlin”. “[http://coll.mfn-berlin.de/u/; 56f9c0](http://coll.mfn-berlin.de/u/;56f9c0)”. {ZMB}.  
Lectotype ♀ of *C. ciliatus* Friese – “CHILE; CONCEPC; 6.11.1904; P. HERBST”. “Trifolium; Blüten.”. “Colletes; ciliatus; 1909 Friese det.”. “Typus”. “Zool. Mus.; Berlin”. “LECTOTYPE; Colletes ciliatus; Friese, 1910; lab. Melo, 2015”. “[http://coll.mfn-berlin.de/u/; 58f9bb](http://coll.mfn-berlin.de/u/;58f9bb)”. {ZMB}.  
Lectotype ♂ of *C. chubutensis* – “Chubut; Patagonia”. “From WFH; Rosenberg”. “Type No.; 22932; U.S.N.M.”. “Colletes; chubutensis; Ckll. TYPE.”. “LECTOTYPE; Colletes chubutensis ♂; Cockerell, 1918; designated R. Ferrari, 2017”. {USNM}. **[hereby designated]**.

*Secondary type specimens:* Paralectotypes ♀ and ♂ of *C. ciliatus* Friese – **CHILE – Region VIII:** Concepción, 17/x/1908, [P.Herbst], 1♂, {ZMB}; idem, except 14/xi/1908, 1♀.

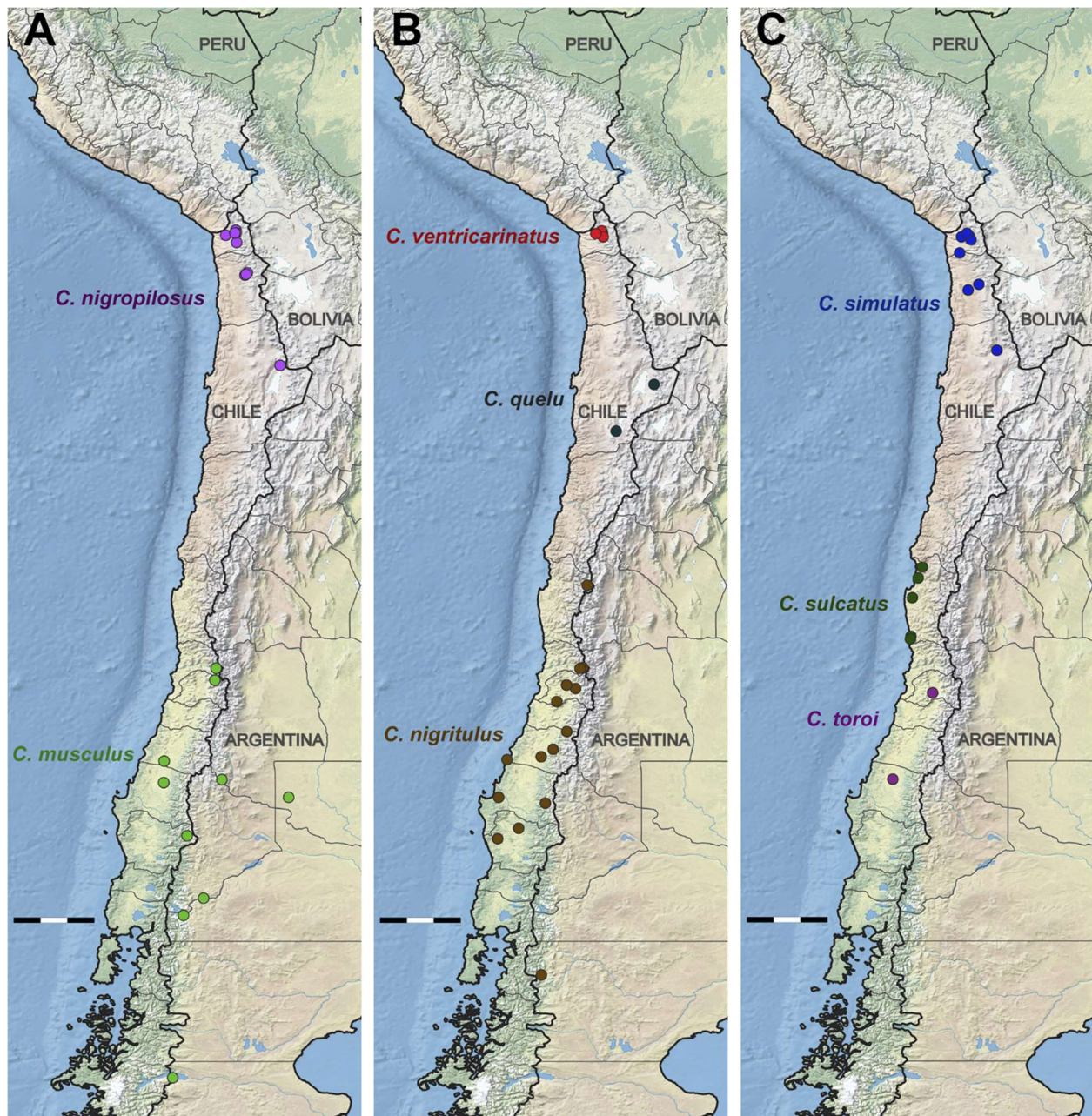
*Additional specimens:* **ARGENTINA – Neuquén:** Neuquén, (-38.935, -68.084), 335m, 14/xi/1908, [P.Herbst], 1♀, {ZMB}. Paso Flores, (-40.549, -70.643), 653m, xi/1964, [A.Giai], 1♂, {MACN}. Pucará, (-38.964, -68.130), 270m, i/1956, 1♀, {KUNHM}. **Río Negro:** Bariloche, (-41.138, -71.274), 824m, xi/1964, [A.Giai], 1♀, {MACN}. **Chubut:** INTA Trevelin site 4, (-43.100, -71.552), 539m, 1/xi/2005, [A.Gravel], 1♀, {PCYU}; idem, except 1/xii/2005, 5♀♀. **CHILE – Region V:** Guardia Vieja, (-32.903, -70.271), 1620m, 17/ix/1964, [L.Peña], 1♀, {AMNH}. **Region Metropolitana:** Farellones, (-33.356, -70.324), 2179m, xi/1994, [Arriagada], 5♂♂, {AMNH}. **Region VII:** El Coigo, xi/1961, [L.Peña], 1♀, {AMNH}. **Region VIII:** Chillán, (-36.364, -72.105), 121m, xii/1994, [Arriagada], 5♀♀5♂♂, {AMNH}. **Region IX:** Lonquimay, (-38.724, -72.601), 117m, 9/xii/1964, 1♀, {AMNH}; idem, except 9/xii/2004, [Ascher & Kawahara], 1♀. Parque Nacional Nahuelbuta, (-37.791, -73.001), 1325m, 31/x/2001, 1♀, [L.Packer], {PCYU}. Río Liucura, 9/xii/2004, [Ascher & Kawahara], 1♀, {AMNH}. **Region XI:** 8km W of Chile Chico, (-46.551, -71.836), 504m, [Schlinder & Irwin], 2♂♂, {PUCV}. Chile Chico, (-46.550, -71.716), 218m, 21/xi/1966, [Schlinger & Irwin], 1♂, {AMNH}; idem, except 22/xi/1966, [M.Irwin], 1♀.

**Range:** Argentina (Neuquén, Río Negro, Chubut), Chile (Regions V–XI). See also Fig. 46A.

**DNA barcode:** Available. BOLD: ACW2084 (2♀♀2♂♂). Barcoded specimens are from Southern Chile and Eastern Argentina and were assigned the same BIN (see Table S1). Distance from the nearest neighbour (*C. cyanescens*): 1.73–4.04%.

**Biogeographic distribution:** South American transition zone: Monte province. Central Chilean sub-region: (Coquimban and Santiagan provinces). Subantarctic sub-region (Maule province). Patagonian sub-region (Patagonian province). Central Chilean and western Argentinean species distributed at altitudes of 100–2200m a.s.l.

**Floral hosts:** Berberidaceae – *Berberis* sp. (Toro 1999). Boraginaceae – *Phacelia* sp. (Toro 1999). Compositae – *Baccharis obovata* Hook. & Arn. (this study). Grossulariaceae – *Ribes magellanicum* Poir. (this study). Leguminosae – *Adesmia* sp. (Toro 1999); *Trifolium repens* L. (this study).



**Figure 46.** Geographic distribution by *Colletes* species. (A) *C. nigropilosus* **n. sp.** and *C. musculus*; (B) *C. ventricarinatus* **n. sp.**, *C. quehu* and *C. nigrutilus*; (C) *C. simulatus* **n. sp.**, *C. sulcatus* and *C. toroi* **n. sp.** Scale bars approximately 300 km.

**Comments:** *Colletes musculus* is widely distributed in Chile, occurring from Guardia Vieja (Region V), in the centre of the country, to as far south as Chile Chico (Region XI). The species is also found in southern Argentina. Across its geographic range, *C. musculus* exhibits some



morphological variation, more markedly in the supraclypeal area (varying from shiny to completely dull), and mesepisternum (varying from finely to moderately coarsely punctate). This variation may well explain why so many different names have been proposed for the same species.

Friese described *C. musculus* based on males and females from Neuquén (Argentina) and Concepción (Chile) collected by Lendl and Herbst, respectively (Friese 1910: 647). Later, Moure examined the type series and designated a female from Neuquén as the species' lectotype (Moure & Urban 2002: 15; see also "Material studied", above). The female lectotypes of *C. musculus* and *C. ciliatus* Friese (not Patton) are morphologically indistinguishable, which means these nominal taxa are subjective synonymies, as previously suggested by Toro (1999: 29). The name *C. musculus*, however, has precedence over *C. biciliatus* (the new name of *C. ciliatus* Friese), following determination by the First Reviser (ICZN 1999; Article 24.2.2).

Examination of the male lectotype of *C. chubutensis* confirmed that this species is also a subjective synonym of *C. musculus* (see Toro 1999: 29). The nomenclatural acts made by Toro (1999) are acknowledged by Ascher & Pickering (2017), but not by Moure & Urban (2002) and Moure *et al.* (2007).

Although the collection date of the lectotype of *C. ciliatus* Friese (November, 6th) does not match that mentioned by Friese in the original description (October), I am herein following Melo's decision of considering Toro & Cabezas' (1977) designation as valid (G. Melo, *pers. comm.*; according to Article 72.4.1.1 of the Code).

### ***Colletes nigrutilus* Friese, 1910**

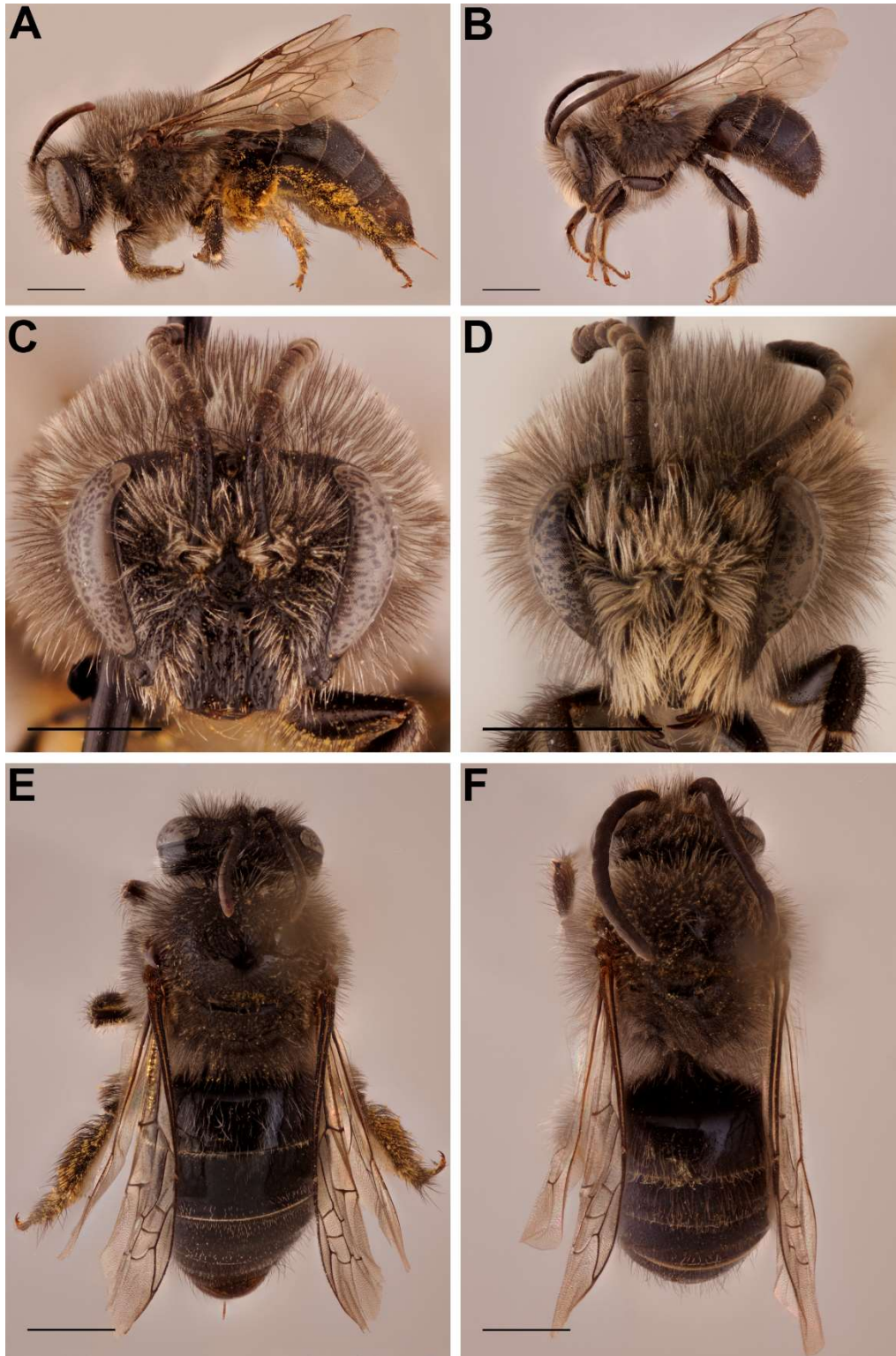
(Figs. 47A–F)

*Colletes nigrutilus* Friese, 1910: 645, 1912: 366; Jaffuel & Pirion 1926: 364; Ruiz 1944: 216; Toro 1986: 123, 1999: 30; Moure & Urban 2002: 15; Moure *et al.* 2007: 685; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

Syntype ♂ (examined). {ZMB}.

*Colletes nigrītula* (sic); Moure 1956: 210.





**Figure 47.** *Colletes nigrifulus* Friese, 1910. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

**Diagnosis:** *Colletes nigrifulus* is distinct among all *Colletes* known to occur in Chile as it is the only black species with a very short malar area, which is approximately 0.4/0.8x (♀/♂) as long as the basal depth of mandible (in all other black species (*C. alocochila*, *C. nigropilosus* n. sp., *C. mastochila*), the malar area is, at least, 1.0/1.5x as long as the basal depth of mandible).

**Redescription:** FEMALE (Figs. 47A, 47C, 47E):

*Dimensions (mm):* Approximate body length 8.4–9.4; head width 3.2–3.5; head length 2.5–2.7; intertegular distance 2.6–3.0; forewing length 7.0–7.7.

*Colouration:* Black except dark-brown on tegula, wing veins (except veins R and C of forewing black), tibial spurs, distitarsi. Reddish-brown on distal half of tarsal claws; marked on distal 1/3 of mandible. Pale-brown on distal 1/5 of ventral surface of mid femur, proximal half of tarsal claws, marginal zones of metasomal sterna.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area evenly shallowly and broadly (1.1x MOD) depressed; adjacent lateral area convex; apicomedial ridge absent. Malar area ~0.4x as long as basal depth of mandible (23:52). F1 ~1.3x as long as its apical width (28:22). UID:LID (68:64). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.2x as long as metanotum (12:62); metapostnotal pits poorly-delimited; posterior transverse carina straight and interrupted medially. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~4x longer than broad (51:13). Outer rami of hind tarsal claws ~1.8x as long as inner rami (22:12). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Mixed off-white and black, plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, paraocular, interantennal, frontal and vertexal areas, pronotal lobe, mesoscutum; such hairs long on metanotum, mesepisternum, metepisternum; entirely black on metanotum (except long), ventral surface of coxae, posteroventral surface of trochanters and front femur, ventral margin of mid femur, S1. Black, erect, moderately long setae on genal area (except plumose near proboscoidal fossa and short behind upper summit of eye), dorsal surface of mid and hind basitarsi and tibiae (except moderately short on mid tibia); such hairs long on posterior surface of front tibia and basitarsus; very long on posterior margin of mid and hind basitarsi. Fulvous, erect, moderately long setae on mandible. Black, suberect, very long hairs,

which are branched only apically on anterior surface of hind femur and tibia. Fulvous, suberect, moderately short, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. T1–T3 with black, erect, short setae; moderately short on T4–T5. S2–S6 with minute, suberect setae on discs; erect, moderately short near marginal zone.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and moderately sparsely punctate (interspaces rugulose); adjacent convex area more coarsely punctate; lower half striate. Malar area finely punctate near eye (interspaces imbricate); impunctate and smooth near mandible. Supraclypeal area imbricate. Paraocular area punctures crowded and coarse below; moderately coarsely and densely punctate above; interspaces smooth and shiny throughout. Frontal area coarsely and densely punctate; interspaces rugulose. Vertexal area rugose near lateral ocellus; sparsely and moderately finely punctate elsewhere. Mesoscutum and scutellum densely and moderately coarsely punctate (except sparsely punctate on mesoscutal mid-posterior area and scutellar mid-longitudinal band); interspaces smooth and shiny (except rugulose on scutellar posterior 1/5). Metanotum densely and moderately finely punctate; interspaces rugose. Mesepisternum punctures crowded and coarse on upper 1/3 (interspaces smooth); moderately coarse and moderately sparse below (interspaces imbricate). Metepisternum rugose above; obliquely striate medially; smooth below. Punctuation on lateral surface of propodeum difficult to discern from the overall rugulose interspaces. Upper area vertical surface of metapostnotum smooth medially. Metasomal terga minutely punctate; interspaces smooth on T1, imbricate on T2–T5, shiny throughout. Metasomal sterna densely and finely punctate (except moderately coarsely punctate on distal half of S6); interspaces imbricate.

MALE (Figs. 47B, 47D, 47F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.4–9.3; head width 2.7–3.1; head length 2.1–2.4; intertegular distance 2.5–2.9; forewing length 6.2–6.9.

*Colouration:* Vein C of forewing, mediotarsi and discs of S2–S4 dark-brown. Stigma and distal 1/3 of distitarsi pale-brown.

*Structure:* Labrum medially convex; convexity not margined by ridges. Clypeal mid-longitudinal area narrowly (0.5x MOD) depressed on upper half; depression broad (=MOD) below. Malar area ~0.8x as long as basal depth of mandible (27:32). F1 ~0.9x as long as its

apical width (23:26). UID:LID (65:52). Genal area concave behind upper summit of compound eyes in lateral view. Horizontal surface of metapostnotum  $\sim 0.2\times$  as long as metanotum (11:54); metapostnotal pits well-delimited. Hind basitarsus  $\sim 4.2\times$  longer than broad (55:13). Outer rami of hind tarsal claws  $\sim 2.1\times$  as long as inner rami (17:8). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 48A, 48B, 48C, respectively.

*Pubescence:* Hairs on lateral slopes of clypeus and supraclypeal area mostly off-white. Genal area, T1, disc of T2 with plumose hairs. Setae on T3 moderately short. Plumose hairs on S1 off-white.

*Surface sculpture:* Clypeal and supraclypeal area with smooth interspaces. Scutellum moderately densely punctate. Mesepisternal punctation moderately coarse throughout. Metasomal terga finely punctate; interspaces smooth throughout. Metasomal sterna minutely punctate.



**Figure 48.** Dorsal view of the male terminalia of *C. nigrutilus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** *Primary type specimen:* Syntype ♂ – “CHILE; CONCEPC.; X 1903; P. HERBST”. “Colletes; nigrutilus; 1909 Friese det.”. “Typus”. “LECTOTYPE; Colletes nigrutilus; Friese, 1910; desig. Melo, 2015”. “<http://coll.mfn-berlin.de/u/58f9be>”. {ZMB}.

*Additional specimens:* **ARGENTINA – Chubut:** INTA Trevelin, (-43.114, -71.590), 688m, 17/i/2006, [A.Gravel], 1♀2♂♂, {PCYU}. **CHILE – Region IV:** E of Aduanas, (-30.138, -70.061), 2706m, 3/ii/2016, [L.Packer], 2♂♂, {PCYU}. **Region V:** E of Río Blanco, (-32.878, -

70.208), 1898m, 30/xii/2008, [L.Packer], 1♂, {PCYU}. El Canelo, (-33.575, -70.445), 865m, xi/1979, [L.Peña], 1♀, {AMNH}; idem, except i/1977, 1♂. Río Blanco, 31/i/1968, [Montenegro], 1♂, {PUCV}. **Region Metropolitana:** Alhué, (-34.027, -71.099), 180m, 17/xii/1987, [L.Peña], 1♂, {PCYU}. **Region VII:** Linares, (-35.847, -71.606), 158m, i/1979, [L.Peña], 1♀, {AMNH}. Tregualemu, (-35.946, -72.739), 55m, 28/xii/2006, [L.Packer], 1♂, {PCYU}; idem, except 17/xii/2006, 1♀. Vado Estero los Molongos, (-35.011, -70.743), 779m, 26/i/2016, [L.Packer], 2♂♂, {PCYU}. Vilches, (-35.570, -71.178), 587m, i/1999, [P.Arce], 1♂, {AMNH}. **Region VIII:** 14km W of Santa Juana, (-37.162, -73.106), 619m, 2/xii/1997, [L.Packer], 3♂♂, {PCYU}. W of Parque Nacional Laguna del Laja, (-37.395, -71.457), 921m, 3/iii/2013, [Postlethwaite & Monckton], 1♀, {PCYU}. **Region IX:** Chacamo, (-38.583, -73.053), 414m, 19/i/1983, [L.Peña], 1♀, {AMNH}. Laguna Galletué, (-38.694, -71.286), 1163m, 10/i/1962, [L.Peña], 1♂, {AMNH}. Victoria, (-38.232, -72.351), 348m, i/1985, [L.Peña], 1♂, {AMNH}.

**Range:** Argentina (Chubut), Chile (Regions IV–IX). See also Fig. 46B.

**Biogeographic distribution:** Central Chilean sub-region: (Coquimban and Santiaguan provinces). Subantarctic region (Maule province). Patagonian sub-region (Patagonian province). Central Chilean and western Argentinean species distributed at altitudes of 0–2800m a.s.l.

**DNA barcode:** Available. BOLD: AAV9330 (4♀♀2♂♂). Barcoded specimens cover most of the latitudinal range of the species; representatives from central Chile and southern Argentina were assigned the same BIN. Distance from the nearest neighbour (*C. flavipilosus* n. sp.): 5.28–6.03%.

**Floral hosts:** Escalloniaceae – *Escallonia pulverulenta* (Ruiz & Pav.) Pers. [Jaffuel & Pirion 1926 (as *E. berteriana* DC.)]; *E. virgata* (Ruiz & Pav.) Pers. (this study). Quillajaceae – *Quillaja saponaria* Molina (Ruiz 1944).

**Comments:** Uncommon species although widely distributed in central Chile. Also found in southern Argentina.

The syntype male from the ZMB that I examined has been labelled as the species' lectotype and should be designated as such in a different study (G. Melo, *pers. comm.*).

***Colletes nigropilosus* Ferrari, new species**

(Figs. 49A–F)

**Diagnosis:** The combination of labral median area depressed and margined by ridges, malar area about 1.5/2.5x (♀/♂) as long as basal depth of mandible, legs with black hairs, and metasomal terga black and not covered with appressed hairs is sufficient to separate *C. nigropilosus* **n. sp.** from all other Chilean species of the genus.

*Colletes nigropilosus* **n. sp.** is most similar to *C. mastochila*, but it differs by having the clypeal lower 1/5 without a mid-longitudinal ridge in female (clypeal lower 1/5 bearing ridge in the female *C. mastochila*); and lateral surface of propodeum with smooth interspaces (lateral surface of propodeum with imbricate interspaces in *C. mastochila*). *Colletes nigropilosus* **n. sp.** is also similar to *C. alocochila*, but these species can be distinguished by the mesoscutal anterior 1/3 densely punctate in the former (mesoscutal anterior 1/3 only moderately densely punctate in *C. alocochila*); and T1 pubescence mostly black in *C. nigropilosus* **n. sp.** (T1 with only off-white hairs in *C. alocochila*).

**Description:** FEMALE (Figs. 49A, 49C, 49E):

*Dimensions (mm):* Approximate body length 10.6; head width 3.4; head length 3.0; intertegular distance 2.7; forewing length 8.0.

*Colouration:* Black except reddish-brown on distal 1/3 of mandible, 1/4 of distitarsi and 2/3 of tarsal claws. Dark-brown on tegula, wing veins (except basal veins of forewing black), stigma, ventral surface of front and hind femurs, anterior surface of mid femur, proximal 3/4 of distitarsi, ventrally reflexed lateral areas of T1–T2. Pale-brown on tibial spurs, proximal 1/3 of tarsal claws, marginal zones of S1–S5.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area evenly shallowly and very narrowly (0.4x MOD) depressed on upper 2/3; adjacent lateral area convex; apicomedial ridge absent. Malar area ~1.6x as long as basal depth of mandible (31:19). F1 ~1.3x as long as its apical width (38:28). UID:LID (71:68).





**Figure 49.** *Colletes nigropilosus* Ferrari, **n. sp.** Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum  $\sim 0.4\times$  as long as metanotum (21:47); metapostnotal pits well-delimited; posterior transverse carina straight and interrupted medially. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 3\times$  longer than broad (49:17). Outer rami of hind tarsal claws  $1.5\times$  as long as inner rami (21:14). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Black, plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, vertexal area, pronotal lobe, mesoscutum, scutellum, anteroventral surface of mid trochanter, ventral margin of mid femur, T2 (except moderately short), S1 (except fulvous); such hairs long on paraocular, frontal and genal areas, metanotum, mesepisternum, metepisternum, anteroventral surface of front trochanter and femur, ventral surface of hind trochanter, T1; very long on interantennal area and upper margin of lateral surface of propodeum. Black, erect, moderately long setae on mandible, posterior surface of front tibia, dorsal surface of mid and hind tibiae and basitarsi (except slightly shorter on mid tibia); such hairs long on posterior margin of basitarsi (except very long on hind basitarsus). Fulvous, suberect, moderately short, thick setae on ventral surface of tarsi; thickest towards distal margin. Black, suberect, long hairs, which are branched only apically on anterior surface of hind femur and tibia. Disc of T3 with black, erect, short setae; longer on T4 and S3–S6; longest on T5. S2 with black, erect, moderately short hairs, which are branched only apically.

*Surface sculpture:* Clypeus densely and moderately finely punctate on mid-longitudinal depression and upper margin; convex area smooth and shiny (except lower  $1/5$  longitudinally striate). Malar area moderately densely punctate medially; finely punctate towards eye; coarser below; interspaces smooth. Supraclypeal area smooth and shiny. Paraocular area punctures crowded and moderately fine below; densely punctate above. Frontal area densely and moderately coarsely. Vertexal area with moderately finely punctures intermingled with minute ones; interspaces smooth. Mesosomal interspaces smooth and shiny throughout. Mesoscutum and scutellum densely and moderately coarsely punctate (except sparsely punctate on mesoscutal mid-posterior area). Metanotum densely and moderately finely punctate. Mesepisternum moderately densely and moderately coarsely punctate (except densely punctate anteriorly episternal groove and near scrobe). Metepisternum rugulose above; obliquely striate medially; smooth below. Lateral surface of propodeum finely and sparsely punctate. Upper area vertical

surface of metapostnotum rugose medially. Metasomal terga minutely and moderately sparsely punctate (except sparsely punctate on T1); interspaces smooth (except imbricate on marginal zones of T1–T5). Metasomal sterna finely punctate and moderately densely punctate (except sparsely punctate on mid-longitudinal band of S2–S5); interspaces imbricate throughout.

MALE (Figs. 49B, 49D, 49F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 8.4; head width 3.1; head length 2.7; intertegular distance 2.2; forewing length 7.5.

*Colouration*: Wing veins pale-brown (except basal veins of forewing black). Distitarsi and marginal zones of T1–T3 dark-brown.

*Structure*: Clypeal mid-longitudinal area evenly broadly (0.4x MOD) depressed on upper 2/3. Malar area ~2.4x as long as basal depth of mandible (41:17). F1 ~1.3x as long as its apical width (32:24). UID:LID (70:62). Genal area concave behind upper summit of compound eyes in lateral view. Horizontal surface of metapostnotum ~0.5x as long as metanotum (20:36); posterior transverse carina sinuous and complete. Hind basitarsus 3x longer than broad (45:15). Outer rami of hind tarsal claws ~1.8x as long as inner rami (26:14). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 50A, 50B, 50C, respectively.

*Pubescence*: Lateral slopes of clypeus and supraclypeal area with off-white hairs. Paraocular and genal areas, pronotal lobe, mesoscutum and scutellum with off-white and black hairs intermixed. T1 covered with very long pubescence. Hairs on S2 ordinarily plumose. Marginal zones of S2–S5 with plumose, erect, short hairs.

*Surface sculpture*: Malar area densely punctate. Supraclypeal area with very sparse moderately coarse punctures. Frontal area punctures crowded. Metepisternum rugulose below; obliquely striate medially. Lateral surface of propodeum with rugulose interspaces. Metasomal terga finely punctate.

**Type material**: *Holotype* ♀ – “CHILE Region I; Chusmiza; 30.x.00 L. Packer”. “Colletes; alocochila; Moure, 1956; det. J.S. Ascher, 2003”. “Colletes”. “HOLOTYPE; Colletes nigropilosus ♀; Ferrari, new species”. {PCYU}.

*Paratypes*: **CHILE – Region XV**: 1.5km SE of Campamento Planchones, (-18.657, -69.537), 3493m, 31/x/2013, [Monckton & Postlethwaite], 1♀, {PCYU}; idem, except 24/ix/2013, [Postlethwaite & Monckton], 1♂. Belén, (-18.467, -69.513), 3297m, 25/x/1952, [L.Peña], 1♂, {DZUP}. E of Zapahuira, (-18.348, -69.552), 3573m, 14/iv/2004, [L.Packer], 1♂, {PCYU}. Zapahuira, (-18.341, -69.595), 3328m, 28/i/1972, [Pasten], 1♂, {PUCV}. Putre, (-18.194, -69.561), 3530m, ii/1948, [G.Kuschel], 2♂♂, {DZUP}; idem, except 30/ix/1970, 1♂, {AMNH}. Road CH-11 km 114.5, 3566m, 3/ii/2013, [Postlethwaite & Monckton], 2♀♀, {PCYU}; idem, except km 117.1, (-18.416, -69.900), 3587m, 29/ix/2015, [L.Packer], 1♂. **Region I**: 82km NE of Huara, (-19.673, -69.179), 3437m, 21/ix/2013, [Almeida & Packer], 1♀, {RPSP}. Codpaquilla, 22/iv/1971, [H.Toro], 1♂, {AMNH}. Chusmiza, (-19.682, -69.188), 3419m, 19/iv/1971, [W.Sielfeld], 1♀, {AMNH}; idem, except, x/1997, [H.Toro], 1♀; idem, except 30/x/2000, [L.Packer], 1♂, {PCYU}. Road CH-15 near Chusmiza turnoff, (-19.721, -69.221), 3304m, 29/x/2013, [Monckton & Postlethwaite], 2♀♀, {PCYU}; idem, except 21/ix/2013, [Postlethwaite & Monckton], 1♂. **Region II**: Guatin, (-22.766, -68.083), 3277m, 23/viii/1982, [L.Peña], 2♂♂, {AMNH}.

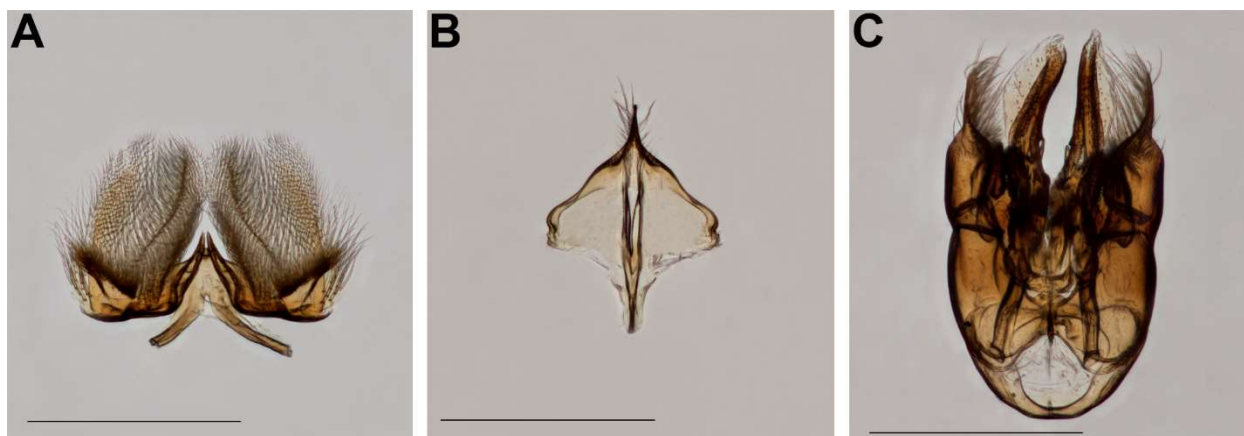
**Range**: Chile (Regions XV, I, II). See also Fig. 46A.

**Biogeographic distribution**: South American transition zone: Desert, Puna and Atacama provinces. Northern Chilean species distributed in the summer rainfall area at altitudes of 3200–3600m a.s.l.

**DNA barcode**: Available. BOLD: ACU7011 (2♀♀1♂). Distance from the nearest neighbour (*C. alocochila*): 8.59–10.09%.

**Floral hosts**: Compositae – *Baccharis scandens* (Ruiz & Pav.) Pers. Leguminosae – *Medicago sativa* L.

**Etymology**: The specific epithet is a reference to the fact that the female *C. nigropilosus* **n. sp.** is entirely covered with black pubescence.



**Figure 50.** Dorsal view of the male terminalia of *C. nigropilosus* **n. sp.** (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Comments:** As with its closest allies (*i.e.* *C. alocochila* and *C. mastochila*), *C. nigropilosus* **n. sp.** is only found across the driest regions of Chile, in the north. Therefore, it is not surprising that most of the material that I studied was misidentified as either *C. alocochila* or *C. mastochila*. *Colletes nigropilosus* **n. sp.** is apparently more common than *C. mastochila*, but not as abundant as *C. alocochila*.

The two male paratypes of *C. nigropilosus* **n. sp.** deposited at the DZUP belong to the type series (allotype and paratype) of *C. alocochila*.

### ***Colletes patagonicus* Schrottky, 1907**

(Figs. 51A–F)

*Colletes patagonicus* Schrottky, 1907: 7, 1913: 236; Cockerell 1918a: 138; Pérez & Cerda 1980: 100; Toro 1986: 123, 1999: 30; Moure & Urban 2002: 16; Moure *et al.* 2007: 685; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

Lectotype ♀ (examined). {ZMB}. **[hereby designated]**

*Colletes rhodaspis* Cockerell, 1909: 397; Schrottky 1913: 236; Ruiz 1944: 205; Moure & Urban 2002: 18; Moure *et al.* 2007: 686. Synonymy proposed by Toro (1999: 30).

Holotype ♀ (examined). {NHM}.

*Colletes patagonica* (sic); Cockerell 1909: 398.

*Colletes rufosignatus* Cockerell, 1918a: 138; Moure & Urban 2002: 19; Moure *et al.* 2007: 687. Synonymy proposed by Toro (1999: 30).

Lectotype ♂ (examined). {USNM}. [hereby designated]

*Colletes campoi* Herbst, 1920: 8; Gazulla & Ruiz 1928: 300; Ruiz 1944: 205. Synonymy proposed by Toro (1999: 30).

Lectotype ♀ (examined). {MCZ}. [hereby designated]

**Diagnosis:** *Colletes patagonicus* is very distinct from all other *Colletes* species due to the ferruginous scutellar and metanotal pubescence (sometimes pale-orange in males), which strongly contrasts with the partially (females) to entirely (males) pale-yellow mesoscutal pubescence. In females, the pale-yellow mesoscutal hairs are intermingled with black ones, increasing the colour contrast.

*Colletes patagonicus* is most similar to *C. flavipilosus* **n. sp.**, but they can be easily differentiated by the characteristics given above (scutellar and metanotal pubescence pale-yellow, as on the mesoscutum in *C. flavipilosus* **n. sp.**); and T2–T5 without appressed hairs in *C. patagonicus* (T2–T5 covered with pale-yellow appressed hairs in *C. flavipilosus* **n. sp.**).

**Redescription:** FEMALE (Figs. 51A, 51C, 51E):

*Dimensions (mm):* Approximate body length 8.0–9.2; head width 2.9–3.3; head length 2.1–2.4; intertegular distance 2.4–2.8; forewing length 6.2–6.9.

*Colouration:* Black except dark reddish-brown marked on tip of mandible. Dark-brown on tegula, wing venation (except vein R of forewing black), stigma, mediotarsi. Pale-brown on distitarsi, marginal zones of T1–T4 and of S1–S5, distal half of tarsal claws. Yellow on proximal half of tarsal claws.

*Structure:* Labrum medially flat and without ridges. Clypeal mid-longitudinal area evenly narrowly (~0.3x MOD) depressed throughout, shallow above, slightly deeper below; adjacent lateral area convex; apicomedial ridge absent. Malar area slightly longer than basal depth of mandible (31:29). F1 1.25x as long as its apical width (30:24). UID:LID (68:62). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded. Horizontal surface of metapostnotum 0.4x as long as metanotum (22:52); propodeal pits poorly-delimited; posterior transverse carina sinuous and narrowly interrupted medially. Posteromedial



surface of front coxa bearing very long spine (0.75x MOD). Posterior hind tibial spur ciliate. Hind basitarsus ~3x longer than broad (46:15). Outer rami of hind tarsal claws 2x as long as inner rami (24:12). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Black, plumose, erect, long on paraocular area; such hairs very long on genal area. Fuscous, plumose, very long on vertexal area, mesepisternum, metepisternum, upper margin of lateral surface of propodeum, ventral surface of mid trochanter and femur, posterior surface of front femur. Interantennal area and mesoscutum with off-white and black hairs intermingled. Ferruginous, plumose, long on scutellum and metanotum, strongly contrasting with the remaining pubescence. Fuscous, erect, moderately short setae on discs of T3–T4, posterior 1/3 of S3–S6; such hairs moderately long on mandible, posterior surface of front tibia and basitarsi, dorsal surface of mid and hind basitarsi and tibiae, T3 laterally, disc of T5; very long on posterior margin of mid and hind basitarsi; T4–T5 laterally. Pale-yellow, suberect, thick setae near distal margin of ventral surface of tarsi. Pale-yellow, erect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. On T1 pale-yellow, plumose, very long; shorter on T2. S1–S2 with pale-yellow, erect, moderately short hairs, which are branched only apically.

*Surface sculpture:* Clypeal mid-longitudinal depression moderately finely and densely punctate; sparsely punctate on adjacent convex area; lower 1/5 longitudinally striate. Supraclypeal area imbricate. Malar area sparsely punctate medially; interspaces imbricate throughout. Paraocular area densely and moderately coarsely punctate below; sparser and finer above. Frontal, vertexal and upper genal areas densely and moderately finely punctate; interspaces finely rugulose. Mesoscutum moderately coarsely punctate; dense on anterolateral area; sparse on disc; moderately sparse on posterior margin; interspaces smooth and shiny (except imbricate on anterior margin). Scutellum moderately sparsely finely punctate on anterior 1/3; denser and coarser on posterior 2/3; interspaces smooth and shiny. Metanotum densely punctate; interspaces rugose. Mesepisternum moderately densely punctate; interspaces imbricate. Metepisternum obliquely striate medially; rugulose above and below. Lateral surface of propodeum sparsely finely punctate; interspaces imbricate. Upper area of vertical surface of metapostnotum imbricate medially. T1–T5 finely shallowly punctate; interspaces imbricate. Posterior margins of S2–S6 moderately densely punctate.



**Figure 51.** *Colletes patagonicus* Schrottky, 1907. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

MALE (Figs. 51B, 51D, 51F). As in female, except for usual secondary sexual characteristics and as follows:

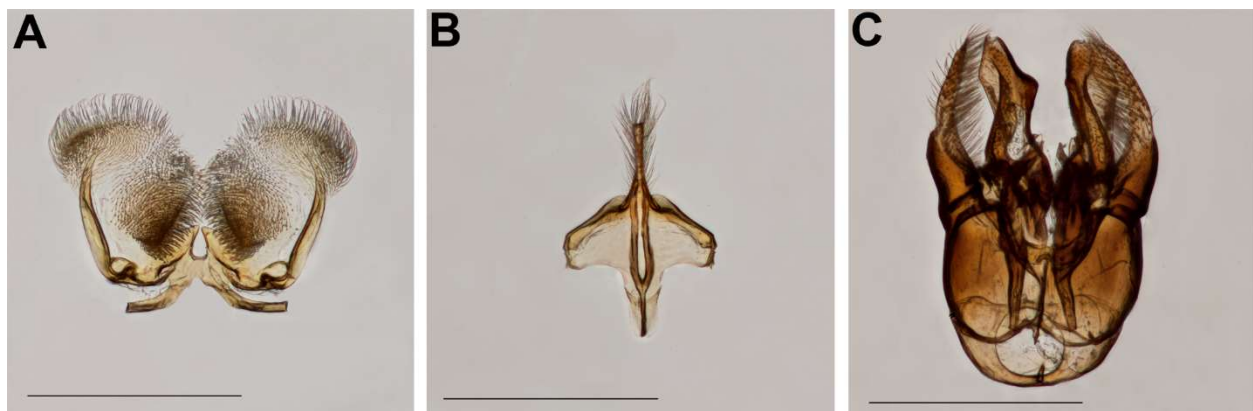
*Dimensions (mm)*: Approximate body length 6.1–6.9; head width 2.4–2.7; head length 2.0–2.2; intertegular distance 2.1–2.4; forewing length 5.4–5.8.

*Colouration*: Wing veins pale-brown. Metasomal sterna dark-brown (lighter on disc). Pale-brown marginal zones of metasomal sterna broader.

*Structure*: Clypeal mid-longitudinal depression broad (= MOD). Malar area 3x as long as basal depth of mandible (33:11). F1 ~1.2x as long as its apical width (28:24). UID:LID (64:54). Genal area concave behind upper summit of compound eyes in lateral view. Horizontal surface of metapostnotum 0.4x as long as metanotum (24:60). Posteromedial surface of front coxa without spine. Hind basitarsus 5.3x longer than broad (69:13). Outer rami of hind tarsal claws ~1.5x as long as inner rami (22:14). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 52A, 52B, 52C, respectively.

*Pubescence*: Pale-yellow on face (except black on paraocular area), posterior half of genal area, vertexal middle area, mesoscutum, mesepisternum, metepisternum, legs. Sparser on ventral surface of hind tibia. Longer on T2–T5.

*Surface sculpture*: Upper clypeal margin densely punctate. Supraclypeal area with some coarse punctures. Lateral surface of propodeum rugulose. T1–T5 moderately coarsely punctate; interspaces smooth.



**Figure 52.** Dorsal view of the male terminalia of *C. patagonicus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** *Primary type specimens:* Lectotype ♀ of *C. patagonicus* – “Patagonia; Rio Caleufú”. “patagonicus; ♀ Schrottky”. “Colletes; patagonicus; 1910 Schrottky”. “Typus”. “Coll.; Friese”. “Zool. Mus.; Berlin”. “LECTOTYPE; Colletes patagonicus ♀; Schrottky, 1907; designated R. Ferrari, 2017”. {ZMB}. [hereby designated]. Holotype ♀ of *C. rhodaspis* – “Syn.; type”. “B. M. TYPE; HYM.; 17.a.349”. “Patagonia; V. del Lago Xanco.; Chubut.; 1903–359.”. “Colletes ♀; rhodaspis; Type Cockerell”. “Holo.; type”. “♀ HOLOTYPE; Colletes rhodaspis; Cockerell 1909: 397; by original designation; det. D. Notton 2016”. {NHM}. Lectotype ♂ of *C. rufosignatus* – “Chubut; Patagonia”. “From WFH; Rosenberg”. “Type No.; 22933; U.S.N.M.”. “Colletes; rufosignatus; Ckll. TYPE.”. “LECTOTYPE; Colletes rufosignatus ♂; Cockerell, 1918; designated R. Ferrari, 2017”. {USNM}. [hereby designated]. Lectotype ♀ of *C. campoi* – “CHILE; Tolhuaca; departem.; Mariluan; 16.I.1991”. “Type!; Colletes; campoi; ♀ P. Herbst”. “P. Herbst; Collection”. “Type; 17213”. “MCZ-ENT; 00017213”. “LECTOTYPE; Colletes campoi ♀; Herbst, 1920; designated R. Ferrari, 2017”. {MCZ}. [hereby designated].

*Additional specimens:* **ARGENTINA – Chubut:** INTA Trevelin site 1, (-43.127, -71.562), 386m, 20/xii/2005, [A.Gravel], 1♀, {PCYU}. **CHILE – Region X:** 6km N of Río Negro, (-40.754, -73.223), 61m, 9/xii/1985, [A.Roig-Alsina], 1♀1♂, {MACN}. **Region XI:** Melinka, (-43.895, -73.743), 56m, i/1969, [G.Barria], 1♀, {AMNH}. **Region XII:** Est. Brazo Norte, 23/i/1972, [V.Perez], 1♀, {AMNH}. Laguna Amarga, (-50.976, -72.769), 81m, 7/xii/1966, [Schlinger & Irwin], 1♀, {AMNH}. Laguna Azul, (-50.875, -72.726), 225m, xii/1978, [W.Sielfeld], 1♀, {AMNH}. Punta Arenas, 1/i/1979, (-53.159, -70.950), 81m, [W.Sielfeld], 1♂, {AMNH}.

**Range:** Argentina (Río Negro, Chubut, Santa Cruz), Chile (Regions X–XII). See also Fig. 10A.

**Biogeographic distribution:** Subantarctic sub-region (Valdivian Forest and Magellanic provinces). Patagonian sub-region (Patagonian province). Southern South American species distributed at altitudes of 0–400m a.s.l.

**DNA barcode:** Available. BOLD: AAO3408 (1♀1♂). The two barcoded specimens from southern Chile and Argentina were assigned the same BIN (see Table S1). Distance from the nearest neighbour (*C. flavipilosus* n. sp.): 3.22–3.82%.

**Floral hosts:** Lamiaceae – *Nepeta racemosa* Lam. [Pérez & Cerda 1980 (as *N. mussinii* Spreng. ex Henckel)]. Leguminosae – *Trifolium repens* L. (this study).

**Comments:** Uncommon species restricted to southern South America.

I examined the type specimens of the species placed under synonymy with *C. patagonicus* by Toro (1999) and herein confirm his decisions (see above). In an alternative classification, *C. rhodaspis* and *C. rufosignatus* are treated as valid; the former is also considered the senior synonym of *C. campoi* (Moure & Urban 2002). The great variation in body size exhibited by *C. patagonicus* across its geographic range combined with the fact the ferruginous pubescence on the scutellum and metanotum fades over time, likely explain the reason why so many different names have been proposed for the same species.

### ***Colletes quelu* Rojas & Toro, 1993**

(Figs. 53A–C)

*Colletes quelu* Rojas & Toro, 1993: 85; Toro 1999: 30; Moure *et al.* 2007: 686; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

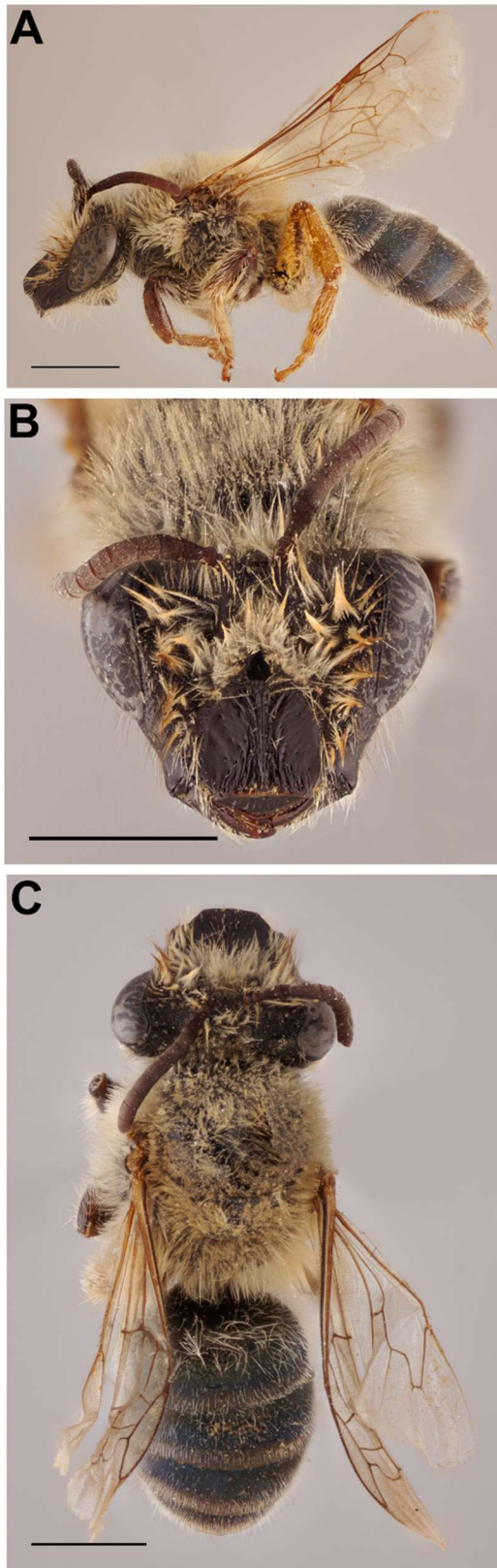
Holotype ♀ (examined). {AMNH}.

**Diagnosis:** *Colletes quelu* can be diagnosed through the following combination of characters: clypeal mid-longitudinal area carinate, mesoscutal pubescence pale-yellow, hind tibia pale-orange, and metasomal terga metallic blue.

*Colletes quelu* is most similar to *C. guanta*, however, the females of these species can be distinguished by the comparatively shorter malar area, ~1.5x as long as basal depth of mandible, in *C. quelu* (malar area 1.8x as long as basal depth of mandible in *C. guanta*); comparatively longer F1, ~1.4x as long as its apical width, in *C. quelu* (F1 ~1.2x as long as its apical width in *C. guanta*); and hind tibia pale-orange in *C. quelu* (hind tibia dark-brown in *C. guanta*).

**Redescription:** FEMALE (Figs. 53A, 53C, 53E):

*Dimensions (mm):* Approximate body length 7.5–7.8; head width 3.1–3.2; head length 2.2–2.3; intertegular distance 2.2–2.3; forewing length 6.0–6.2.



**Figure 53.** *Colletes quelu* Rojas & Toro, 1993. Female: (A) habitus, lateral view; (B) face, frontal view; (C) habitus, dorsal view. Scale bars = 2mm.



*Colouration:* Black except metallic greenish-blue on discs of T1–T5 (except marginal zones metallic purplish). Metallic dark-blue on mesoscutum, metasomal sterna (except marginal zones pale-brown). Pale-orange on front and mid tarsomeres 2–5, distal ring of hind femur, hind tibia and tarsus, proximal half of tarsal claws. Dark-brown on tegula, wing veins (except vein R of forewing), anterior surface of front tibia. Reddish-brown on distal 1/2 of tarsal claws; marked on distal 1/3 of mandible.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area with a strong, complete carina; adjacent area declivous. Malar area ~1.5x as long as basal depth of mandible (36:25). F1 ~1.4x as long as its apical width (36:26). UID:LID (65:66). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.4x as long as metanotum (22:54); metapostnotal pits poorly-delimited; posterior transverse carina absent. Posteromedial surface of front coxa bearing very short spine (0.2x MOD). Posterior hind tibial spur ciliate. Hind basitarsus ~3.7x longer than broad (55:15). Outer rami of hind tarsal claws ~4x as long as inner rami (23:6); inner rami extremely reduced. Posterolateral area of S6 flat and lacking carina; marginal zone not depressed.

*Pubescence:* Pale-yellow, plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, interantennal, frontal and genal areas, mesoscutum, scutellum, metepisternum, posteroventral surface of front trochanter and femur, ventral surface of mid trochanter, ventral margin of mid femur, S1; such hairs long on vertexal area, metanotum, mesepisternum, ventral surface of hind coxa, T1; very long on upper margin of lateral surface of propodeum. Paraocular area with pale-yellow and black hairs intermingled. Pale-yellow, erect, moderately short setae on posterior surface of front basitarsus, dorsal surface of mid basitarsus and hind basitarsus and tibia; such hairs very long on posterior margin of hind basitarsus. Front and mid tibiae with pale-yellow, suberect, short setae on dorsal surface; such hairs thick on ventral surface of mid and hind tarsi (thickest towards distal margin). Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T2 with pale-yellow, plumose, erect, moderately short hairs. T3–T5 and S3–S6 covered with pale-yellow, erect, moderately short setae. S2 with pale-yellow, erect, moderately short hairs, which are branched only apically.

*Surface sculpture:* Clypeus longitudinally striate near mid-longitudinal carina and lower margin; declivous area smooth and shiny. Malar area with moderately coarse punctures intermingled with minute ones; interspaces smooth. Supraclypeal area somewhat rugulose. Paraocular area moderately finely punctate; punctures crowded below; densely punctate above. Frontal area densely and moderately coarsely punctate; interspaces rugulose. Vertexal area finely and moderately sparsely punctate; interspaces smooth (except rugose near ocellus and occipital margin). Mesoscutum moderately finely and moderately densely punctate (except sparsely punctate on mid-posterior area); interspaces smooth and shiny. Scutellum densely and moderately coarsely punctate; interspaces smooth on anterior 1/3; rugulose on posterior 2/3. Metanotum densely and moderately finely punctate; interspaces somewhat rugulose. Mesepisternum densely and moderately coarsely punctate; interspaces imbricate. Metepisternum rugose above; obliquely striate medially; rugulose below. Lateral surface of propodeum with fine punctures difficult to discern from the rugulose interspaces. Upper area of vertical surface of metapostnotum rugose medially. Metasomal terga finely and densely punctate (except moderately densely punctate on T1); interspaces imbricate (except rugulose on T2–T3 anteriorly). Metasomal sterna finely and moderately densely punctate; interspaces imbricate.

MALE: Unknown.

**Material studied:** *Primary type specimen:* Holotype ♀ – “HOLO; TIPO”. “CHILE, II Reg; Talabre XII-; 1959, H. Toro”. “Colletes; quelu; Toro & Rojas 93”. “AMNH\_IZC 00324330”. {AMNH}.

*Secondary type specimen:* Paratype ♀ – **CHILE – Region II:** Talabre, xii/1959, [H.Toro], 1 ♀, {AMNH}.

*Additional specimens:* **CHILE – Region II:** Parque Nacional Llullaillaco, (-24.962, -69.096), 3767m, 8/iv/2010, [Ugarte], 2 ♀♀, {PCYU}. Talabre, (-23.323, -67.838), 3554m, 6/xii/1992, [E.Chiappa], 1 ♀, {AMNH}.

**Range:** Chile (Region II). See also Fig. 46B.

**Biogeographic distribution:** South American transition zone: Atacama province. Northern Chilean species distributed in the summer rainfall area at altitudes of 3500–3800m a.s.l.

**DNA barcode:** Available. BOLD: ACK8809 (2♀♀). Distance from the nearest neighbour (*C. fulvipes*): 3.25–3.41%.

**Floral hosts:** Unknown.

**Comments:** Extremely rare species found only at very high elevations (3500m a.s.l. or higher) in Region II. Although a series of bee surveys have been carried out at the type locality (Talabre, Region II) and nearby areas by a series of melittologists (*e.g.* H. Toro, E. Chiappa, L. Packer, S. Monckton), the male *C. quelu* has not been collected.

***Colletes rutilans* Vachal, 1909**

(Figs. 54A–F)

*Colletes rutilans* Vachal, 1909: 52; Cockerell 1918b: 207; Toro 1986: 123, 1999: 30; Moure & Urban 2002: 20; Moure *et al.* 2007: 687; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

Holotype ♀ (examined). {MNHP}.

**Diagnosis:** The combination of malar area shorter than basal depth of mandible and marginal zones of T1–T5 covered with appressed hairs is sufficient to distinguish *C. rutilans* from all other Chilean species of the genus, except *C. lucens*. However, *C. rutilans* is different in having a ferruginous mesoscutal pubescence (mesoscutal pubescence pale-yellow in *C. lucens*), and T1 densely and moderately finely punctate (punctuation on T1 inconspicuous in *C. lucens*).

**Redescription:** FEMALE (Figs. 54A, 54C, 54E):

*Dimensions (mm):* Approximate body length 8.7–9.5; head width 3.2–3.5; head length 2.4–2.6; intertegular distance 2.1–2.5; fore wing length 6.6–7.2.



**Figure 54.** *Colletes rutilans* Vachal, 1909. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

*Colouration:* Black except dark-brown on wing veins, stigma, dorsal surface of tarsi (except distitarsi pale-brown). Reddish-brown on distal half of tarsal claws; marked on distal half of mandible (except subapical tooth entirely black). Pale-orange on tegula, proximal half of tarsal claws. Pale-yellow on tibial spurs, marginal zones of S1–S5. Pale-brown on marginal zones of T1–T4.

*Structure:* Labrum medially flat and without ridges. Clypeal mid-longitudinal area neither depressed nor carinate; adjacent lateral area convex; apicomedial ridge absent. Malar area  $\sim 0.4x$  as long as basal depth of mandible (21:50). F1  $\sim 1.3x$  as long as its apical width (30:23). UID:LID (68:59). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum half as long as metanotum (25:50); metapostnotal pits well-delimited; posterior transverse carina straight and complete. Posteromedial surface of front coxa bearing very short spine ( $0.25x$  MOD). Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 3.1x$  longer than broad (41:13). Outer rami of hind tarsal claws  $\sim 1.9x$  as long as inner rami (27:14). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Ferruginous, branched, erect, moderately long on pronotal lobe, mesoscutum, scutellum, metanotum; such hairs long on mesepisternum, metepisternum, upper margin of lateral surface of propodeum (except very long), posteroventral surface of front trochanter and femur, ventral surface of mid and hind trochanters, ventral margin of mid femur. Pale-yellow, branched, erect, moderately long on mandible, lateral slopes of clypeus and supraclypeal area, paraocular, frontal and genal (except short behind eye, long near proboscoidal fossa) areas, ventral surface of front and mid coxae, T1, S1–S2 (except moderately short on S2). Pale-yellow, suberect, short setae on dorsal surface of front and mid tibiae; such hairs very long on posterior margin of mid and hind basitarsi. Pale-yellow, erect, moderately short on posterior surface of front tibia and basitarsus, dorsal surface mid basitarsus and hind basitarsus and tibia; such hairs thick on ventral surface of mid and hind tarsi (thickest towards distal margin). Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. Discs of T2–T5 with pale-yellow, suberect, minute setae; T4–T5 also with some erect, moderately short setae; marginal zones of T1–T5 with bright-yellow appressed hairs. S3–S6 with pale-yellow, erect, moderately short setae on discs; marginal zones with plumose, suberect hairs.

*Surface sculpture:* Clypeus evenly densely and moderately coarsely punctate; integument longitudinally striate throughout. Malar area substrigulate. Supraclypeal area densely and moderately coarsely punctate; interspaces rugulose but somewhat shiny. Paraocular area punctures crowded and moderately coarse below; slightly sparser and finer above. Frontal area punctures crowded and moderately coarse. Vertexal area densely punctate with moderately coarse and fine punctures intermingled (interspaces smooth); integument rugose near occipital area. Mesoscutum densely and moderately coarsely punctate on anterior half; sparser and coarser on posterior half; interspaces smooth and shiny throughout. Scutellum punctures crowded and moderately coarse. Metanotal punctation difficult to discern from overall rugose interspaces. Mesepisternum moderately densely punctate with coarse and minute punctures intermingled; interspaces smooth and shiny (except rugulose anteriorly to episternal groove). Metepisternum rugose above and below; obliquely striate medially. Lateral surface of propodeum rugose. Upper area of vertical surface of metapostnotum transversely striate medially. T1–T2 densely (except sparsely on T1 mid-longitudinally) and moderately finely punctate. T3–T5 finely and densely punctate; interspaces smooth and shiny throughout. S1 with very sparse fine punctures. S2–S6 finely and moderately densely punctate (except sparsely punctate mid-longitudinally); interspaces imbricate.

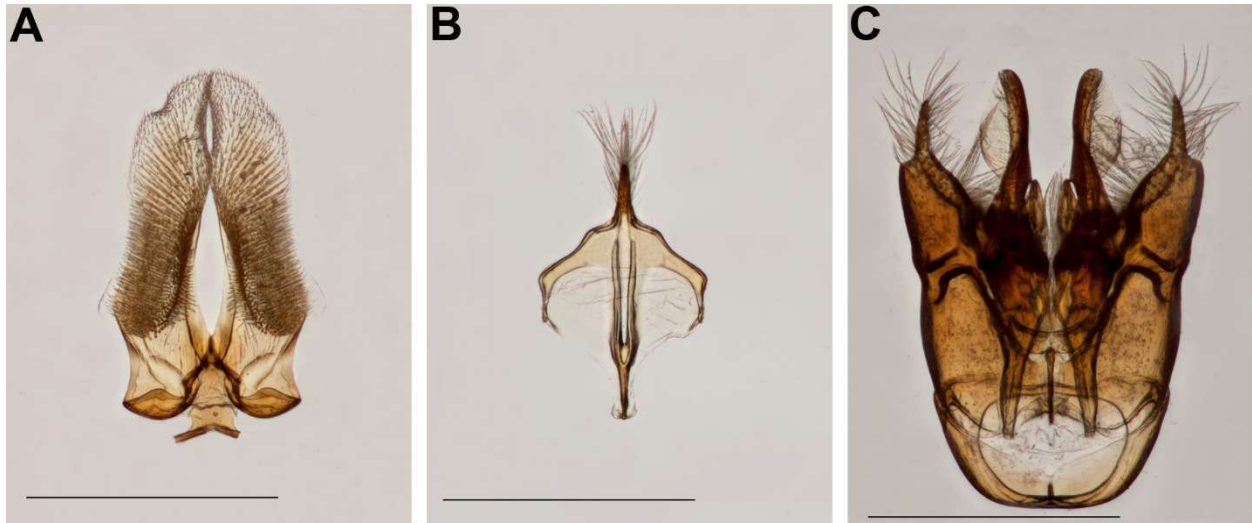
MALE (Figs. 54B, 54D, 54F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.2–8.9; head width 2.7–3.0; head length 2.1–2.2; intertegular distance 1.9–2.2; fore wing length 6.3–6.8.

*Colouration:* Mandibular subapical tooth mostly reddish-brown (except apex black). Dorsal surface of hind tibia and discs of metasomal sterna dark-brown.

*Structure:* Malar area 0.9x as long as basal depth of mandible (27:30). F1 ~1.3x as long as its apical width (30:23). UID:LID (64:50). Genal area concave behind upper summit of compound eyes in lateral view. Horizontal surface of metapostnotum ~0.9x as long as metanotum (26:30). Posteromedial surface of front coxa without spine. Hind basitarsus ~3.9x longer than broad (43:11). Outer rami of hind tarsal claws ~1.4x as long as inner rami (17:12). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 55A, 55B, 55C, respectively.





**Figure 55.** Dorsal view of the male terminalia of *C. rutilans*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Pubescence:* Genal hairs long behind eye. Dorsal surface of front and mid tibiae with erect setae. Disc of T2 with plumose, erect hairs.

*Surface sculpture:* Supraclypeal area punctures crowded. Mesoscutal anterior half moderately densely punctate. Mesepisternal area just below scrobe with rugulose interspaces. Mid-longitudinal band of T1 moderately densely punctate. T4–T6 with imbricate interspaces.

**Material studied:** *Primary type specimen:* Holotype ♀ – “-Baños-; (Ecuad.); R. Haensch S.”. “HOLOTYPE”. “Coll. ♀; rutilans; Vach.”. “MUSEUM PARIS; COLL. J. VACHAL 1911”. “Colletes; rutilans; Vach.”. {MNHP}.

*Additional specimens:* **CHILE – Region XV:** Lluta valley, (-18.325, -69.836), 1391m, 7/ii/1965, [L.Peña], 2♀♀1♂, {AMNH}. **Region II:** Calama, (-22.443, -68.942), 2252m, i/1995, [Arriagada], 1♀, {AMNH}; idem, except ii/1992, 2♂♂. Lasana, (-22.266, -68.621), 2701m, xi/1996, [U.Peña], 5♂♂, {AMNH}. 20km N of San Pedro de Atacama, (-22.689, -68.250), 3132m, 26/iii/2000, [L.Packer], 1♂, {PCYU}; idem, except 29/iii/2000, 1♀. San Pedro de Atacama, (-22.910, -68.211), 2422m, 20/ii/1960, [L.Peña], 1♀, {AMNH}. **ECUADOR – Loja:** Loja, (-4.007, -79.192), 2168m, 25/x/2014, [A.Pauly], 4♀♀, {PCYU}; idem, except 13/x/2014, 1♀.

**Range:** Chile (Regions XV, I, II), Ecuador (Loja, Tungurahua), Peru (La Libertad). See also Fig. 10B.

**Biogeographic distribution:** Brazilian sub-region – Pacific dominion (Cauca province). South American transition zone (Desert and Atacama provinces). Western South American species distributed at altitudes of 1300–3200m a.s.l.

**DNA barcode:** Available. BOLD: AAI9251 (2♀♀). Only specimens from northern Chile were barcoded.

**Floral hosts:** Compositae – *Taraxacum* sp. (this study).

**Comments:** *Colletes rutilans* is widely distributed in western South America: besides the specimens from northern Chile, I also examined six females from the type locality (Loja Province, Ecuador), including the holotype. However, the species has also been recorded as far north as the Colombian Department of Magdalena, close to the border with Venezuela (Ascher & Pickering 2017). Specimens from Ecuador and Chile are morphologically indistinguishable.

The female holotype is missing the metasoma; the head and mesosoma (including legs and wings) are in good condition.

### ***Colletes simulatus* Ferrari, new species**

(Figs. 56A–F)

**Diagnosis:** The combination of clypeal mid-longitudinal area depressed, paraocular and mesoscutal pubescence with off-white and black hairs intermixed, T1 with coarse punctation, and T2–T5 covered with yellow appressed hairs differentiates *C. simulatus* **n. sp.** from all other Chilean species of *Colletes*.

*Colletes simulatus* **n. sp.** is most similar to *C. atacamensis*, however, these species can be easily distinguished from each other by the paraocular and mesosomal pubescence with off-white and black hairs intermixed in *C. simulatus* **n. sp.** (paraocular and mesosomal pubescence with pale-yellow hairs only, in *C. atacamensis*); comparatively longer malar area, ~1.5x as long as

basal depth of mandible, in the female *C. simulatus* **n. sp.** (malar area ~1.3x as long as basal depth of mandible in the female *C. atacamensis*); and mesoscutum densely punctate ( $i=0.5d$ ) in the male *C. simulatus* **n. sp.** [mesoscutum moderately densely punctate ( $i=1-1.5d$ ) in the male *C. atacamensis*].

**Description:** FEMALE (Figs. 56A, 56C, 56E):

*Dimensions (mm):* Approximate body length 8.8; head width 3.1; head length 2.4; intertegular distance 2.1; forewing length 7.2.

*Colouration:* Black except pale-yellow on tibial spurs, wing veins (except vein R of forewing pale-brown), stigma, distitarsi, tarsal claws (except bright-yellow on proximal 1/3), marginal zones of T1–T5 and S1–S5. Dark-brown on tegula, dorsal surface of tibiae and tarsi (except distitarsi), ventral area of T1–T3, metasomal sterna (except mid-longitudinal band pale-brown). Reddish-brown marked on distal half of mandible.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area deeply and narrowly ( $0.4x$  MOD) depressed on upper half; depression shallow and broad ( $=MOD$ ) below; adjacent lateral area convex; apicomedial ridge absent. Malar area ~1.5x as long as basal depth of mandible (44:29). F1 ~1.3x as long as its apical width (38:28). UID:LID (65:61). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum ~0.4x as long as metanotum (29:68); metapostnotal pits well-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus 4x longer than broad (48:12). Outer rami of hind tarsal claws ~1.3x as long as inner rami (24:18). Posterolateral area of S6 flat and lacking carina; marginal zone depressed.

*Pubescence:* Off-white, plumose, erect, long on lateral slopes of clypeus and supraclypeal area, genal area (except moderately short behind eye), mesepisternum, metepisternum, ventral surface of front coxa, posteroventral surface of front trochanter and femur, ventral surface of mid and hind trochanters, T1. Mixed off-white and back hairs on paraocular, interantennal, frontal and vertexal areas, pronotal lobe, mesoscutum, scutellum, metanotum, upper margin of lateral surface of propodeum. Pale-yellow, erect, moderately long setae on mandible, dorsal surface of mid and hind tibiae and basitarsi; fulvous, long on posterior surface of front tibia, dorsal surface

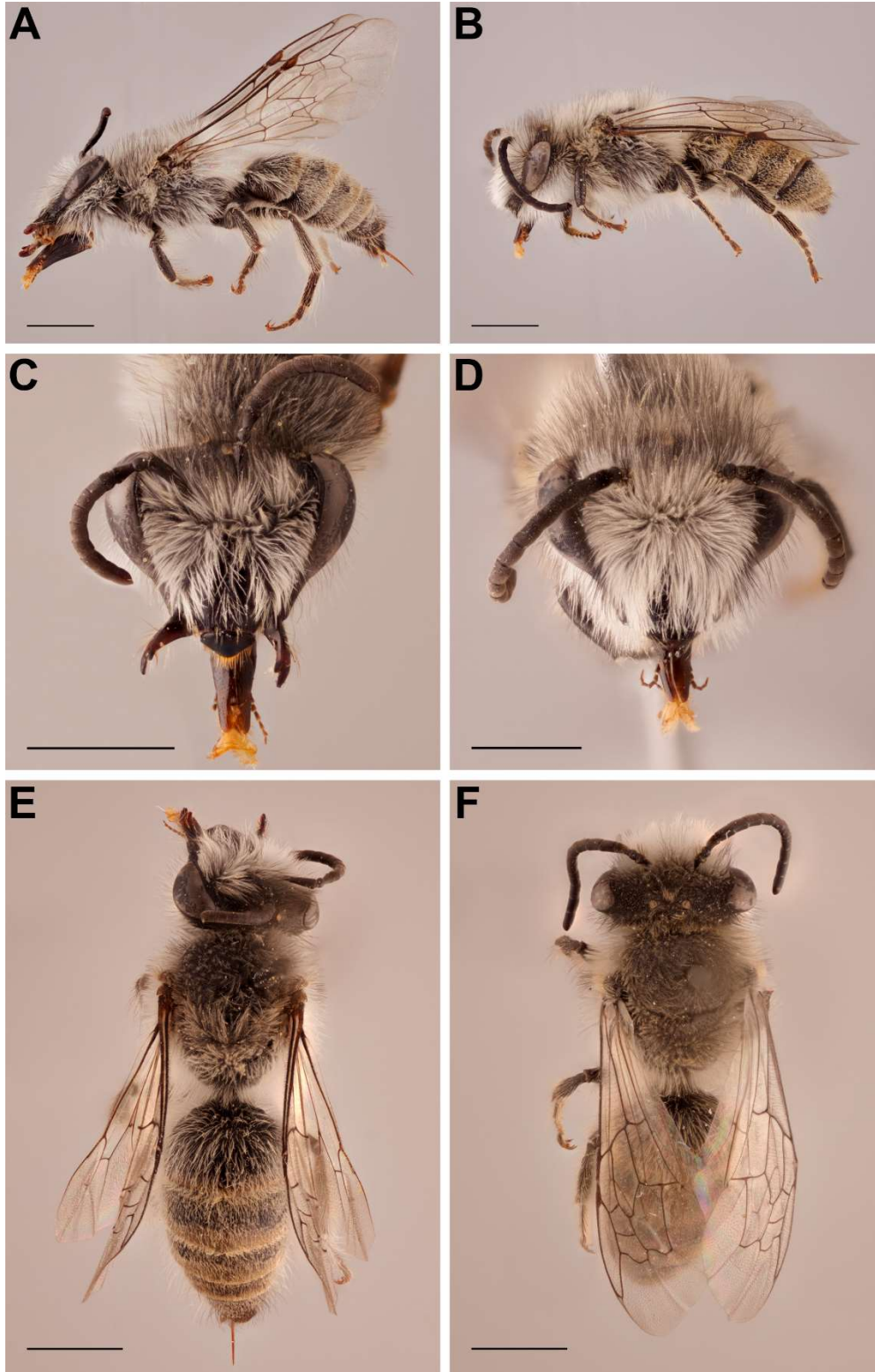
of front basitarsi, posterior margin of mid basitarsi; such hairs very long on posterior margin of hind basitarsus. Bright-yellow, suberect, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T2–T5 with pale-yellow, dense appressed hairs; T4–T5 also with very sparse black setae (longer on T5). S2 with pale-yellow, erect, short hairs, which are branched only apically. Discs of S3–S6 with pale-yellow, erect, moderately short setae; marginal zones with plumose, suberect hairs (except S6).

*Surface sculpture:* Clypeal mid-longitudinal depression punctures crowded and moderately fine (except moderately dense below); adjacent convex area largely impunctate. Malar area longitudinally striate. Supraclypeal area with very sparse coarse punctures; interspaces smooth and shiny. Paraocular area densely punctate; moderately coarsely punctate below; slightly finer above; interspaces smooth and shiny throughout. Frontal area punctures crowded and moderately coarse. Vertexal area densely and moderately coarsely punctate (except finely punctate near eye). Mesoscutum, scutellum and mesepisternum densely and coarsely punctate (except sparsely punctate on mesoscutal mid-posterior area); interspaces smooth and shiny. Metanotum densely and moderately coarsely punctate; interspaces rugulose but somewhat shiny. Metepisternum rugulose above; obliquely striate medially; smooth below. Lateral surface of propodeum sparsely and moderately coarsely punctate; interspaces rugose. Upper area of vertical surface of metapostnotum rugose medially. T1 densely punctate; moderately coarse punctures intermingled with fine ones. T2 densely and minutely punctate; anterior 1/3 with minute punctures intermingled with moderately fine ones. T3–T5 sparsely and minutely punctate. Metasomal sterna sparsely and finely punctate (except moderately coarsely punctate on S6); interspaces imbricate.

MALE (Figs. 56B, 56D, 56F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 7.6; head width 3.0; head length 2.3; intertegular distance 2.0; forewing length 6.7.

*Colouration:* Dorsal surface of tibiae, metasomal sterna black. Wing veins, stigma, dorsal surface of distitarsi dark-brown.



**Figure 56.** *Colletes simulatus* Ferrari, **n. sp.** Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

*Structure:* Clypeal mid-longitudinal area evenly deeply depressed; depression narrow (0.6x MOD) on upper half, wide below (= MOD). Malar area ~2.1x as long as basal depth of mandible (54:26). F1 ~1.1x as long as its apical width (34:30). UID:LID (67:56). Horizontal surface of metapostnotum ~0.4x as long as metanotum (23:62). Hind basitarsus ~3.7x longer than broad (44:12). Outer rami of hind tarsal claws ~1.7x as long as inner rami (20:12). Marginal zone of S6 flat not depressed. S7, S8 and genital capsule as in Figs. 57A, 57B, 57C, respectively.

*Pubescence:* Mesepisternum and metepisternum with off-white and black hairs intermixed. Posterior margin of mid basitarsus with pale-yellow setae. S2 with plumose hairs only.

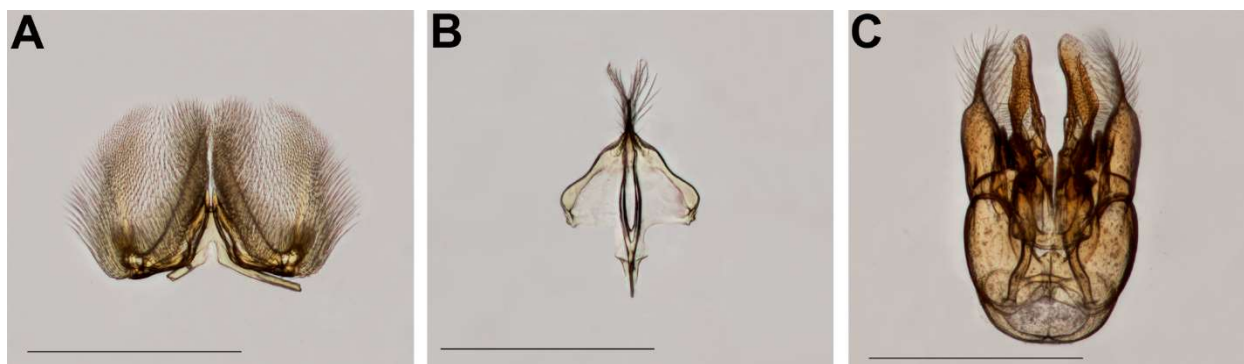
*Surface sculpture:* Supraclypeal area densely punctate. Vertexal area punctures crowded. Lateral surface of propodeum moderately densely punctate. T1 with coarse punctures intermingled with moderately fine ones. Punctuation on T2–T3 composed of moderately coarse punctures intermingled with fine ones. T4–T5 densely and finely punctate. S6 finely punctate.

**Type material:** *Holotype* ♀ – “CHILE: Region XV, 1.5km SE Campamento Planchones; -18.6988, -69.60847. 3030m; 31.x-30.xi.2013. White; S. Monckton & J. Postlethwaite”. “CCDB-22014; D10”. “HOLOTYPE; *Colletes simulatus* ♀; Ferrari, new species”. {PCYU}.

*Paratypes:* **CHILE – Region XV:** 30km W of Zapahuira, (-18.333, -69.894), 1799m, 3/iv/2000, [L.Packer], 1♂, {PCYU}. Pucará Belén, (-18.472, -69.527), 3178m, 1/xi/2013, [S.Monckton], 1♂, {PCYU}. Tambo, (-18.356, -69.620), 3235m, 12/iv/2004, [L.Packer], 1♂, {PCYU}. Tignamar, (-18.567, -69.488), 3416m, 24/ix/2013, [L.Packer], 1♂, {PCYU}. **Region I:** 23km E of Pozo Almonte, (-20.251, -69.555), 1081m, 22/ix/2013, [Almeida & Packer], 5♂♂, {RPSP}. E of Pozo Almonte, (-20.252, -69.581), 1057m, 6/ii/2013, [Postlethwaite & Monckton], 1♂, {PCYU}. Mamiña, (-20.062, -69.222), 2758m, 29/x/2013, [S.Monckton], 1♂, {PCYU}. Sobraya, (-18.580, -70.052), 570m, 10/xi/1955, 1♀, {KUNHM}. Vale de Camarones, (-19.004, -69.856), 735m, 14/vii/1976, [Porter & Calmbacher], 1♀, {AMNH}. Mamiña, (-20.062, -69.222), 2757m, 25/iv/2015, [L.Packer], 1♀, {PCYU}. **Region II:** Lasana, xi/1996, (-22.266, -68.621), 2701m, [U.Peña], 1♂, {AMNH}.

**Range:** Chile (Regions XV, I, II). See also Fig. 46C.





**Figure 57.** Dorsal view of the male terminalia of *C. simulatus* **n. sp.** (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Biogeographic distribution:** South American transition zone: Desert and Atacama provinces. Northern Chilean species distributed in the summer rainfall area at altitudes of 500–3500m a.s.l.

**DNA barcode:** Available. BOLD: AAV8097 (2♀♀4♂♂). Distance from the nearest neighbour (*C. nigropilosus* **n. sp.**): 10.46–11.26%.

**Floral hosts:** Leguminosae – *Caesalpinia* sp.

**Etymology:** *Colletes simulatus* **n. sp.** has been largely misidentified as *C. atacamensis* in most bee collections that houses specimens of the former, which is not surprising given these species are very similar to each other. “Simulatus”, therefore, means that the species has been “pretending” to be a different species all this time.

**Comments:** Uncommon species found only in northern Chile.

### ***Colletes sulcatus* Vachal, 1909**

(Figs. 58A–F)

*Colletes sulcatus* Vachal, 1909: 58; Toro 1999: 24; Moure & Urban 2002: 21; Moure *et al.* 2007: 688; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

Lectotype ♂ (examined) designated by Moure & Urban (2002: 21). {MNHP}.

*Colletes araucariae* Friese, 1910: 649, 1912: 367; Claude-Joseph 1926: 125; Jaffuel & Pirion 1926: 363; Ruiz & Stuardo 1935: 322; Ruiz 1944: 203; Stephen 1954: 161; Torchio 1965: 183; Roig-Alsina 1991: 259; Toro 1999: 26; Moure & Urban 2002: 3; Moure *et al.* 2007: 678; Montalva & Ruz 2010: 21; Ascher & Pickering 2017. [new synonymy]

Lectotype ♀ (examined) designated by Moure & Urban (2002: 3). {ZMB}.

**Diagnosis:** Females are recognizable by the diagnostic combination of malar area ~1.3x as long as basal depth of mandible, mesoscutal pubescence with pale-yellow hairs only, posterior hind tibial spur ciliate, and T1 minutely punctate and covered with appressed hairs. Males are similar to females, but they have malar area ~2.2x as long as basal depth of mandible and T1 finely and moderately densely punctate and not covered with appressed hairs.

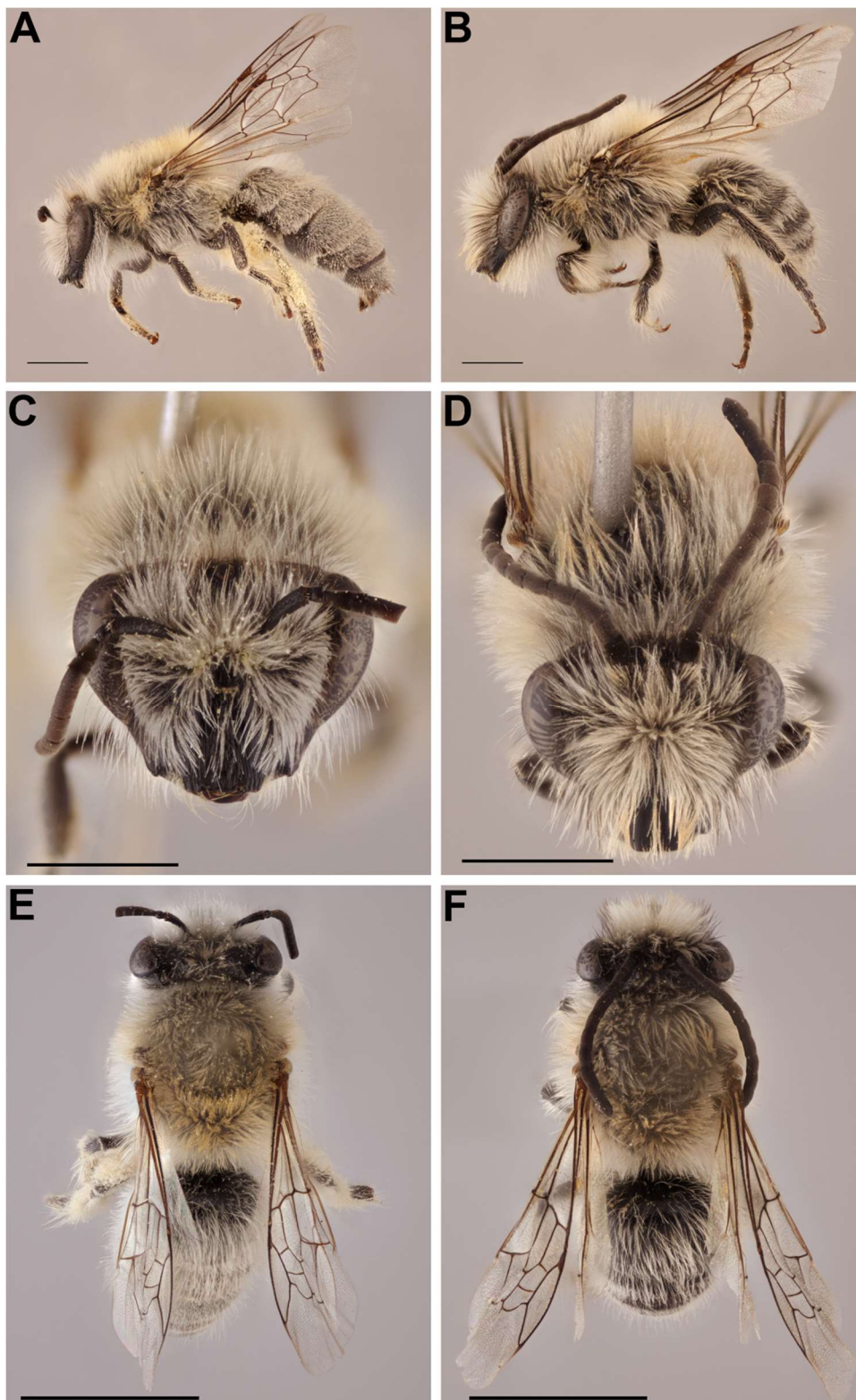
*Colletes sulcatus* is very similar to *C. longiceps*, but their females can be differentiated by the clypeal mid-longitudinal area deeply depressed in the former (clypeal mid-longitudinal area not depressed in the latter); and posterior hind tibial spur ciliate in *C. sulcatus* (spur pectinate in *C. longiceps*). The males can be distinguished by the paraocular area with pale-yellow and black hairs intermixed, in *C. sulcatus* (paraocular area with pale-yellow hairs only, in *C. longiceps*); and mesepisternal interspaces smooth in *C. sulcatus* (mesepisternal interspaces rugulose in *C. longiceps*).

**Redescription:** FEMALE (Figs. 58A, 58C, 58E):

*Dimensions (mm):* Approximate body length 7.8–8.8; head width 3.0–3.4; head length 2.5–2.8; intertegular distance 2.6–3.0; forewing length 6.4–7.0.

*Colouration:* Black except dark-brown on tegula, vein C of forewing, tarsomeres 4–5 (except distal 1/4 of distitarsi pale-brown), ventrally reflexed lateral areas of T1–T4, lateral margin of S6. Pale-brown on wing veins (except vein C of forewing), stigma, proximal half of tarsal claws. Reddish-brown on distal half of tarsal claws; marked on distal 1/3 of mandible. Yellow on tibial spurs, marginal zones of metasomal sterna.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area evenly deeply depressed; depression narrow (0.4x MOD) on upper 1/4, broad (0.9x MOD) on middle 2/4; adjacent lateral area convex; apicomедial ridge absent.



**Figure 58.** *Colletes sulcatus* Vachal, 1909. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

Malar area  $\sim 1.3\times$  as long as basal depth of mandible (42:33). F1  $\sim 1.3\times$  as long as its apical width (31:24). UID:LID (67:62). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum  $\sim 0.5\times$  as long as metanotum (25:48); metapostnotal pits well-delimited; posterior transverse carina straight and complete. Posteromedial surface of front coxa bearing short spine ( $0.4\times$  MOD). Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 3\times$  longer than broad (45:14). Outer rami of hind tarsal claws  $\sim 2\times$  as long as inner rami (15:8). Posterolateral area of S6 flat and bearing ridge; marginal zone depressed.

*Pubescence:* Pale-yellow, plumose, erect, moderately long on lateral slopes of clypeus and supraclypeal area, interantennal area, pronotal lobe, mesoscutum, scutellum, ventral surface of mid trochanter, ventral margin of mid femur, S1; such hairs long on genal area (except very long near proboscidal fossa), metanotum, mesepisternum, metepisternum, anteroventral surface of front trochanter and femur, ventral surface of hind trochanter; very long on upper margin of lateral surface of propodeum. Paraocular, frontal and vertexal areas with pale-yellow and black hairs intermingled. Pale-yellow, suberect, short setae on dorsal surface of front and mid tibiae; such setae thick on ventral surface of mid and hind tarsi (thickest towards distal margin). Pale-yellow, erect, moderately long setae on dorsal surface of mid and hind basitarsi and hind tibiae; such setae long on posterior surface of front basitarsus and posterior margin of mid and hind basitarsi. Pale-yellow, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T1–T5 covered with pale-yellow, dense appressed hairs; T1–T2 also with plumose, erect, long hairs (except shorter on T2); T3–T5 also with pale-yellow, erect, moderately short setae (intermingled with black ones on T5). S2 with pale-yellow, erect, moderately short hairs, which are branched only apically. S3–S5 with pale-yellow, suberect, short setae restricted to posterior 1/3; marginal zone of S3 with plumose hairs; S6 with fulvous setae restricted to lateral margin.

*Surface sculpture:* Clypeal mid-longitudinal depression with very sparse fine punctures; adjacent convex area longitudinally striate; integument shiny throughout. Malar area moderately coarsely punctate medially; finely punctate near eye; substrigulate near mandible. Supraclypeal area rugulose but somewhat shiny. Paraocular area densely punctate; moderately finely punctate below (except coarser towards antennal socket and supraclypeal area); finely punctate above; interspaces smooth throughout. Frontal area densely and moderately coarsely punctate;

interspaces smooth. Vertexal area with minute punctures intermingled with moderately fine ones; punctation moderately dense (except dense near ocellus); interspaces smooth and shiny. Mesosomal integument smooth throughout. Mesoscutum moderately coarsely and moderately densely punctate (except sparsely punctate on mid-posterior area). Scutellum coarsely and densely punctate (except posterior 1/3 punctures crowded and moderately coarse). Metanotum punctures crowded and moderately fine. Mesepisternum coarsely and moderately densely punctate (except densely punctate near scrobe). Metepisternum rugose above; obliquely striate medially; smooth below. Lateral surface of propodeum sparsely and moderately finely punctate; interspace smooth on anterior half; rugulose elsewhere. Upper area of vertical surface of metapostnotum transversely striate medially. Metasomal terga minutely punctate; interspaces smooth throughout. Metasomal sterna sparsely and finely punctate on posterior 2/3 (except S6 evenly moderately finely punctate); interspaces imbricate.

MALE (Figs. 58A, 58C, 58E). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 6.9–7.7; head width 2.9–3.2; head length 2.4–2.6; intertegular distance 2.2–2.5; forewing length 6.1–6.7.

*Colouration*: Tegula black. Wing veins dark-brown (except vein R of forewing black). Distitarsi dark- brown throughout. S6 black throughout.

*Structure*: Clypeal mid-longitudinal area evenly shallowly depressed; depression narrow (0.5x MOD) on upper half, broad (0.8x MOD) on lower half. Malar area ~2.2x as long as basal depth of mandible (45:20). F1 ~1.3x as long as its apical width (26:25). UID:LID (68:56). Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.6x as long as metanotum (23:41). Posteromedial surface of front coxa without spine. Hind basitarsus ~4.3x longer than broad (52:12). Outer rami of hind tarsal claws ~1.5x as long as inner rami (14:9). Posterolateral area of S6 without ridge; marginal zone not depressed. S7, S8 and genital capsule as in Figs. 59A, 59B, 59C, respectively.

*Pubescence*: Setae on dorsal surface of mid and hind basitarsi moderately long. Appressed hairs on T1–T5 restricted to marginal zones. Disc of S2 with plumose hairs. Setae on discs of S3–S6 evenly distributed; marginal zones of S3–S5 with a band of plumose, erect, short hairs (except moderately short on S3).

*Surface sculpture:* Clypeal mid-longitudinal depression densely punctate; adjacent convex area smooth; striation restricted to lower margin. Supraclypeal area with a few moderately fine punctures; interspaces smooth. Vertexal area densely punctate. Scutellum moderately finely punctate. Anterior 1/3 of lateral surface of propodeum densely punctate. Upper area of vertical surface of metapostnotum smooth. Metasomal terga finely and sparsely punctate. S6 finely punctate.

**Material studied:** *Primary type specimens:* Lectotype ♂ of *C. sulcatus* – “Chili; 63”. “MUSEUM PARIS; Chili; COLL. O. SICHEL 1867”. “Colletes ♂; sulcatus; Vach.”. “TYPE”. “Colletes; sulcatus; Vach”. “LECTOTYPE; Colletes sulcatus ♂; Vachal, 1909; labelled R. Ferrari, 2017”. {MNHP}. Lectotype ♀ of *C. araucariae* – “CHILE; CONCEPC.; 7.III 1908; P HERBST”. “Colletes; araucariae; 1909 Friese det.”. “Type”. “Coll.; Friese”. “LECTOTYPE; Colletes araucariae; Friese, 1910; lab. Melo, 2015”. “<http://coll.mfn-berlin.de/u/;58f9b3>”. {ZMB}.

*Secondary type specimens:* Paralectotypes ♂♂ of *C. sulcatus* – **CHILE** – 1863, 4♂♂, {MNHP}.

*Additional specimens:* **CHILE – Region IV:** 7km N of Los Vilos, (-31.849, -71.493), 75m, 11/x/2003, [M.Irwin], 1♂, {BBSL}. Coquimbo, (-29.961, -71.330), 4m, [Gay], 1♀, {MNHP}. Guampulla, (-30.429, -70.977), 565m, 19/x/2001, [Packer & Fraser], 1♀, {PCYU}. Islon, (-29.896, -71.190), 94m, 28/xi/1955, [R.Wagenknecht], 1♀, {KUNHM}. La Serena, (-29.896, -71.253), 15m, 23/i/1955, [R.Wagenknecht], 1♀2♂♂, {KUNHM}; idem, except 19/xi/1955, 1♀; idem, except 8/xii/1955, 1♀. Los Vilos, (-31.918, -71.511), 18m, 4/x/2013, [L.Packer], 6♂♂, {PCYU}; idem, except 11/v/2010, [Packer & Fraser], 1♂; idem, except (-31.744, -71.500), 40m, 12/xi/2002, [Grixti & Zayed], 1♂. Quebrada Seca, (-30.561, -71.447), 229m, 11/x/2002, [Grixti & Zayed], 2♂♂, {PCYU}.

**Range:** Chile (Region IV). See also Fig. 46C.

**Biogeographic distribution:** Central Chilean sub-region (Coquimban province). Central Chilean species distributed at altitudes of 0–600m a.s.l.

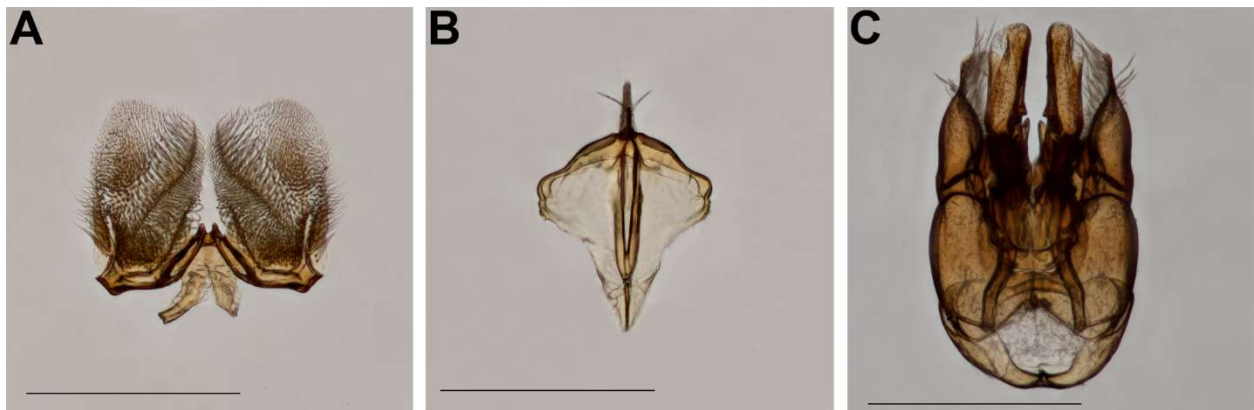


**DNA barcode:** Available. BOLD: AAO3474 (4♂♂). Distance from the nearest neighbour (*C. gilvus*): 9.36–9.98%.

**Floral hosts:** Loasaceae – *Loasa tricolor* Ker Gawl (this study). The following records were originally attributed to *C. araucariae* by Toro (1999): Leguminosae – *Adesmia* sp.; Loasaceae – *Huidobria fruticosa* Phil. [as *Loasa fruticosa* (Phil.) Urb. & Gilg]; Malvaceae – *Cristaria integerrima* Phil. (as *C. foliosa* Phil.).

**Comments:** This is an uncommon species with seemingly restricted geographic range within Chile.

Examination of the lectotypes of *C. sulcatus* (male) and *C. araucariae* (female) indicate that the latter is a junior synonym of the former. This is an interesting case where a commonly mentioned nominal taxon in the literature happens to be a synonym of a nearly completely neglected one (see the synonymy list, above).



**Figure 59.** Dorsal view of the male terminalia of *C. sulcatus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

***Colletes toroi* Ferrari, new species**

(Figs. 60A–F)

**Diagnosis:** Females can be diagnosed by the overall pale-yellow pubescence, clypeal lower 1/3 with mid-longitudinal ridge, and posterior hind tibial spur pectinate. Males are recognizable through the combination of malar area  $\sim 2x$  as long as basal depth of mandible, mesoscutum with pale-yellow hairs only; and T1 densely ( $i < d$ ) and moderately finely punctate.

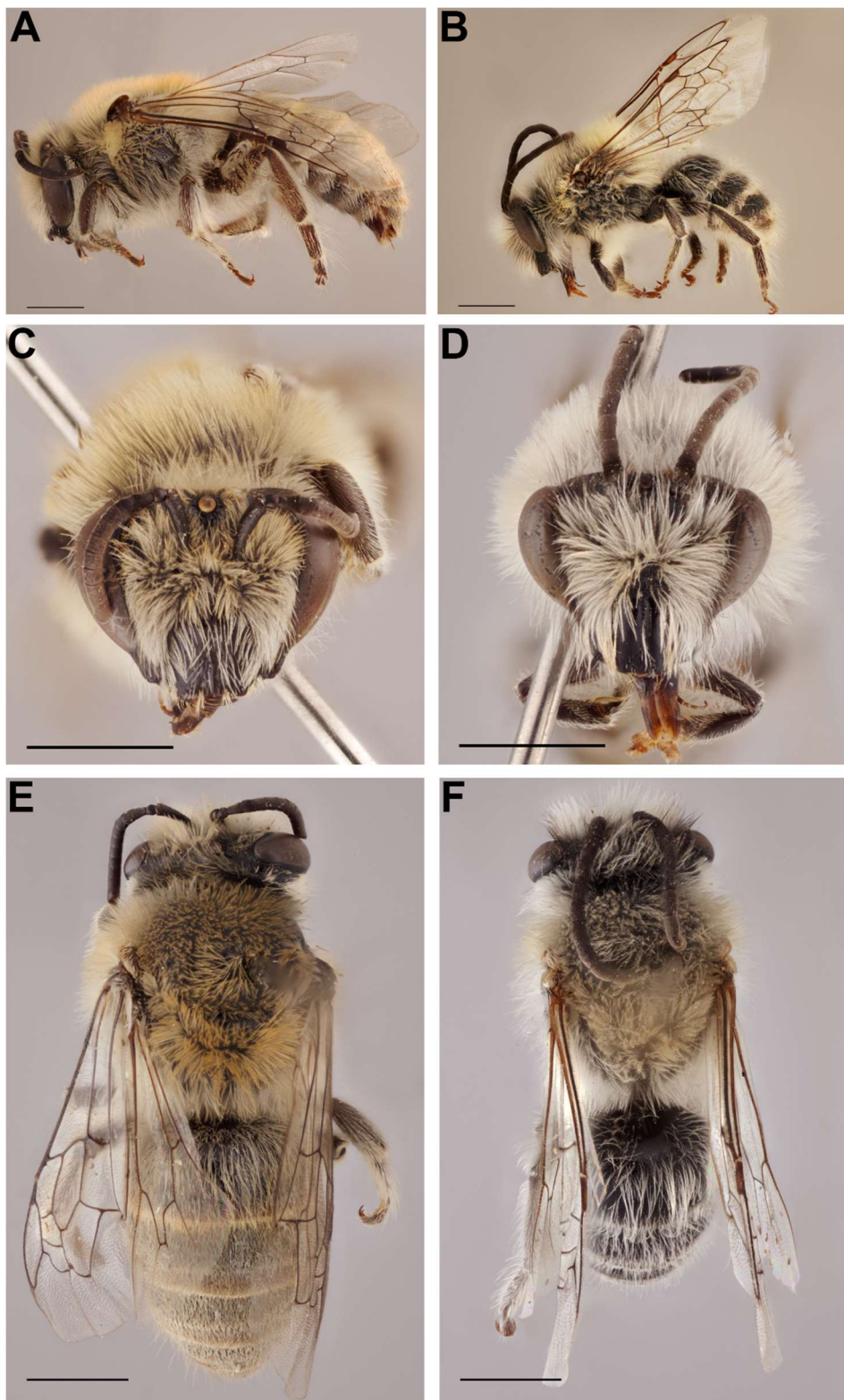
*Colletes toroi* **n. sp.** is most similar to *C. coquimbensis* **n. sp.**, but their females can be distinguished by the mesoscutal pubescence entirely pale-yellow in the former (mesoscutal pubescence with off-white and black hairs intermixed in *C. coquimbensis* **n. sp.**); and the labral median area swollen in *C. toroi* **n. sp.** (labral median area depressed and margined by ridges in *C. coquimbensis* **n. sp.**). The male *C. toroi* **n. sp.** can be differentiated from the male *C. coquimbensis* **n. sp.** due to its comparatively longer malar area,  $\sim 2x$  as long as basal depth of mandible (malar area  $\sim 1.5x$  as long as basal depth of mandible in *C. coquimbensis* **n. sp.**).

**Description:** FEMALE (Figs. 60A, 60C, 60E):

*Dimensions (mm):* Approximate body length 9.2; head width 3.2; head length 2.5; intertegular distance 2.6; forewing length 6.6.

*Colouration:* Black except dark-brown on tegula, wing veins (except vein R of forewing black), legs (except distitarsi pale-brown), ventrally reflexed lateral areas of T1–T2, S1–S5 (except pale-brown mid-longitudinally), S6 posterolaterally. Pale-yellow on tibial spurs, marginal zone of metasomal sterna. Pale-brown on marginal zones of T1–T5. Reddish-brown on distal half of tarsal claws (except proximal 1/3 bright-yellow); marked on distal half of mandible.

*Structure:* Labrum medially concave; concavity margined by lateral ridges. Clypeal mid-longitudinal area not depressed; adjacent lateral area convex; lower 1/3 bearing mid-longitudinal ridge. Malar area  $\sim 0.9x$  as long as basal depth of mandible (28:32). F1  $\sim 1.1x$  as long as its apical width (25:22). UID:LID (62:59). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum modified into a spine. Horizontal surface of metapostnotum  $\sim 0.5x$  as long as metanotum (17:35); metapostnotal pits well-delimited; posterior transverse carina sinuous and interrupted medially. Posteromedial surface of front coxa bearing long spine (0.65x MOD). Posterior hind tibial spur pectinate.



**Figure 60.** *Colletes toroi* Ferrari, **n. sp.** Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

Hind basitarsus 3x longer than broad (42:14). Outer rami of hind tarsal claws ~2x as long as inner rami (13:7). Posterolateral area of S6 convex but without ridge; marginal zone depressed.

*Pubescence*: Pale-yellow throughout. Plumose, erect, moderately short on pronotal lobe; moderately long on lateral slopes of clypeus and supraclypeal area, paraocular, interantennal and frontal areas, mesoscutum, scutellum, metepisternum, ventral margin of mid femur, S1; such hairs long on genal area near proboscoidal fossa, vertexal area, metanotum, mesepisternum, anteroventral surface of front trochanter and femur, ventral surface of mid and hind trochanters; very long on upper margin of lateral surface of propodeum. Erect, moderately short setae on mandible, dorsal surface of mid and hind basitarsi and hind tibia; such setae moderately long on posterior margin of basitarsi (except very long on posterior one). Suberect, short setae on dorsal surface of front and mid tibiae; such setae thick on ventral surface of mid and hind tarsi (thickest towards distal margin). Suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. Dense, appressed hairs on lateral surface of propodeum (except slightly sparser), T1–T5; T1 also with plumose, erect, long hairs; T2–T5 also with erect, moderately short hairs (except longer on T4–T5). S2 with erect, moderately short hairs, which are branched only apically. Discs of S3–S6 covered with suberect, short setae; marginal zones of S2–S5 with a band of plumose, moderately long hairs.

*Surface sculpture*: Clypeal mid-longitudinal area sparsely and moderately finely punctate (interspaces rugulose); striate below; adjacent convex area with very sparse punctures (interspaces smooth). Malar area densely and moderately finely punctate on upper half; substrigulate on lower half. Supraclypeal area rugulose. Paraocular area densely and moderately coarsely punctate below; punctures crowded and moderately fine above; interspaces smooth throughout. Frontal area densely and moderately finely punctate; interspaces rugulose. Vertexal area minutely punctate; interspaces smooth. Mesosomal interspaces smooth (except when stated otherwise). Mesoscutum moderately coarsely and moderately densely punctate (except sparsely punctate on mid-posterior area). Scutellum densely and moderately coarsely punctate (except posterior 1/4 punctures crowded and moderately fine). Metanotum densely and finely punctate. Mesepisternum densely and coarsely punctate (denser and finer on upper lateral area). Metepisternum rugose above; obliquely striate medially; rugulose below. Lateral surface of propodeum sparsely and moderately finely punctate; interspaces rugulose. Upper area of vertical surface of metapostnotum smooth medially. T1 sparsely and finely punctate; T2–T5 minutely

punctate; interspaces smooth throughout. S2–S5 finely and moderately sparsely punctate (except denser posterolaterally and sparser mid-longitudinally); S6 with a few fine punctures mid-longitudinally; interspaces imbricate throughout.

MALE (Figs. 60B, 60D, 60F). As in female, except for usual secondary sexual characteristics and as follows:

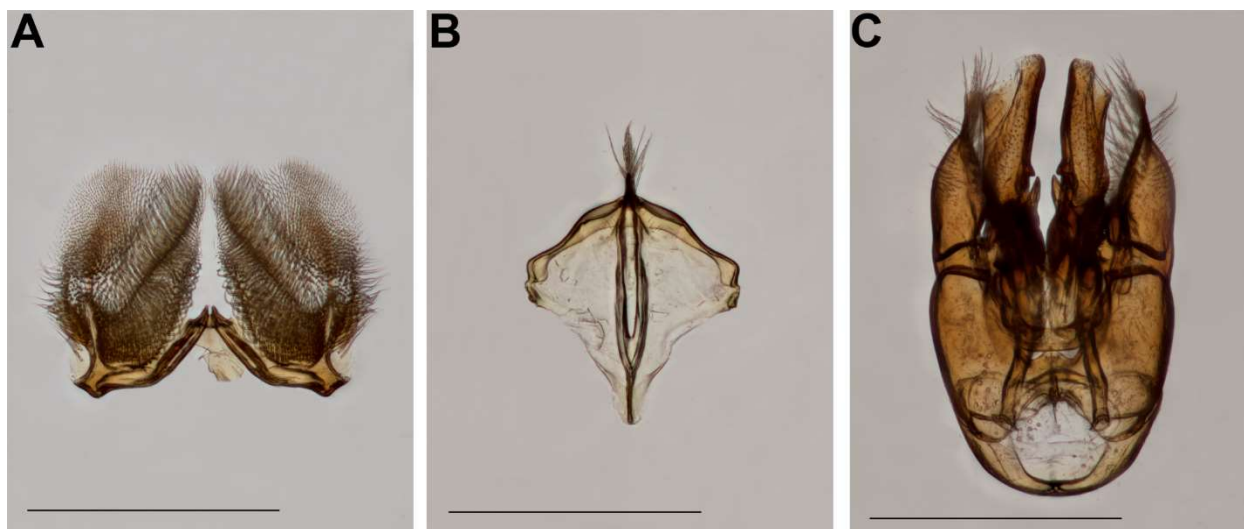
*Dimensions (mm)*: Approximate body length 8.6; head width 3.4; head length 2.6; intertegular distance 2.4; forewing length 7.5.

*Colouration*: Outer margin of tegula pale-yellow. Stigma and wing veins pale-brown (except vein R of forewing black). Proximal 1/3 of tarsal claws pale-orange. Marginal zones of T1–T3 dark-brown. Metasomal sterna evenly dark-brown.

*Structure*: Clypeal mid-longitudinal area evenly deeply and narrowly (0.6x MOD) depressed on upper 3/4; lower 1/3 without mid-longitudinal ridge. Malar area ~2x as long as basal depth of mandible (57:30). F1 ~1.1x as long as its apical width (24:22). UID:LID (73:60). Genal area concave behind upper summit of compound eyes in lateral view. Horizontal surface of metapostnotum ~0.6x as long as metanotum (21:36); posterior transverse carina complete. Posteromedial surface of front coxa spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.3x longer than broad (43:13). Outer rami of hind tarsal claws ~1.8x as long as inner rami (11:6). Posterolateral area of S6 flat; marginal zone not depressed. S7, S8 and genital capsule as in Figs. 61A, 61B, 61C, respectively.

*Pubescence*: Paraocular area with pale-yellow and black hairs intermingled. Genal area and lateral surface of propodeum not covered with appressed hairs. Hairs on pronotal lobe as long as those on mesoscutum. Appressed hairs on T1–T5 restricted to marginal zones. Disc of T2 with moderately long, plumose hairs. Discs of S3–S5 with erect pubescence.

*Surface sculpture*: Clypeal striation restricted to lower margin. Malar area longitudinally striate throughout. Vertexal area densely and moderately coarsely punctate near ocellus; moderately finely and moderately densely punctate near eye. Metanotum punctures crowded. Mesepisternal upper are evenly densely punctate; lower posterior area with rugulose interspaces. Upper area of vertical surface of metapostnotum transversely striate medially. T1 densely and moderately finely punctate; T2–T5 finely punctate. S6 finely and densely punctate laterally.



**Figure 61.** Dorsal view of the male terminalia of *C. toroi* n. sp. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Type material:** *Holotype* ♀ – “CHILE, Ñuble: Chillán; area, “Shangri la”,; Las Trancas, E. Recinto; January 19–22, 1979; 1600 m., L.E. Peña”. “Colletes; araucariae Friese; det. J. S. Ascher”. “AMNH\_ENT; AMNH\_BEE 00074154”. “HOLOTYPE; *Colletes toroi* ♀; Ferrari, new species”. {AMNH}.

*Paratypes:* **CHILE – Region Metropolitana:** Maipo, (-33.724, -70.778), 454m, 20/i/1989, [L.Peña], 1♀, {AMNH}. **Region VIII:** Chillán, (-36.611, -72.129), 111m, 19/i/1979, [L.Peña], 2♂♂, {AMNH}.

**Range:** Chile (Regions Metropolitana, VI–VIII). See also Fig. 46C.

**Biogeographic distribution:** Central Chilean sub-region (Santiago province). Central Chilean species distributed at altitudes of 100–500m a.s.l.

**DNA barcode:** Unavailable.

**Floral hosts:** Unknown.



**Etymology:** This species is named after Haroldo Toro (1934–2002), whose paper on the Chilean *Colletes* (Toro 1999) was an invaluable source of information during the elaboration of this study.

**Comments:** Rare species with a restricted distribution in central Chile, where considerable bee collecting has taken place but only four specimens are known.

***Colletes ventricarinatus* Ferrari, new species**

(Figs. 62A–F)

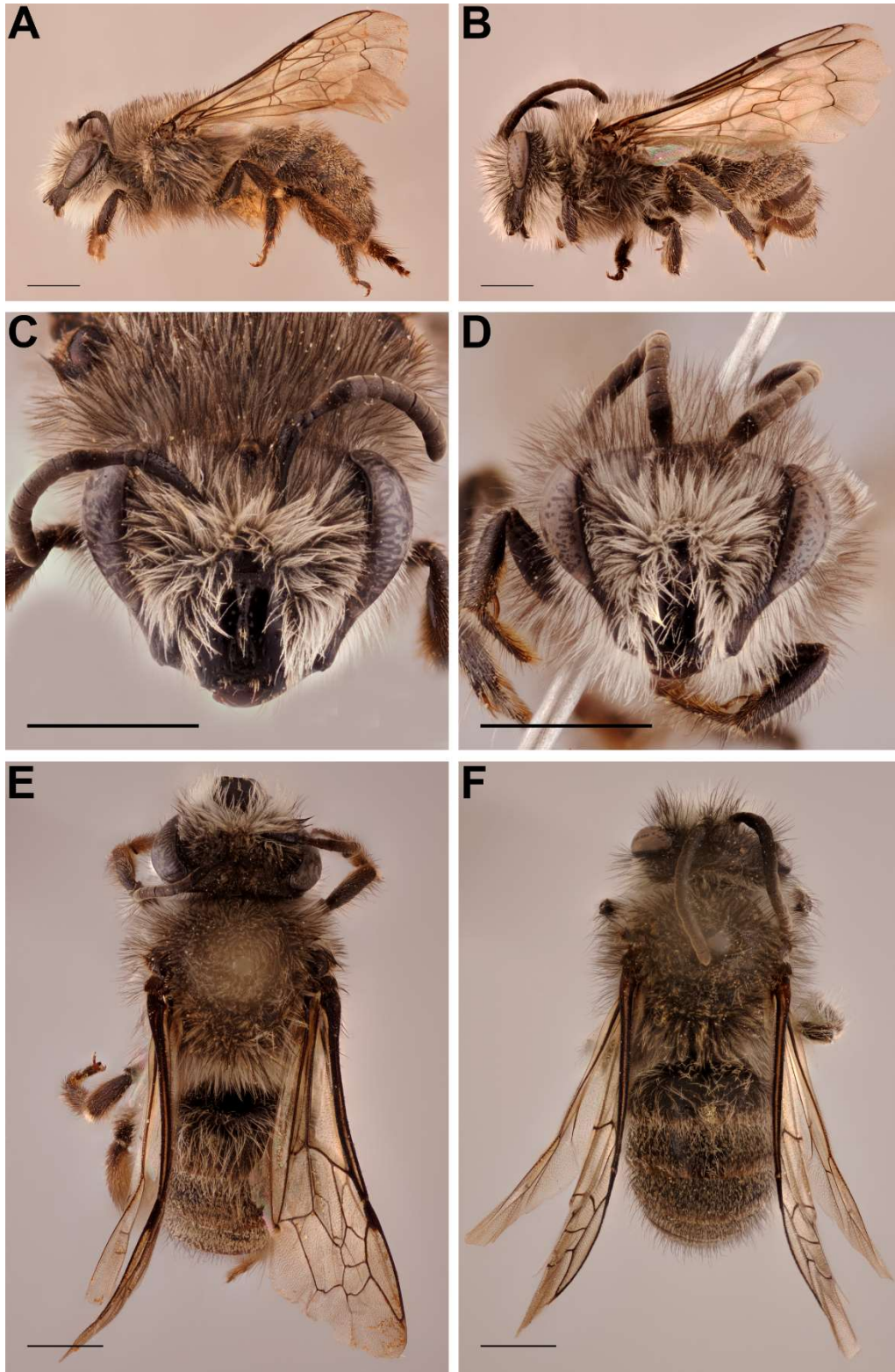
**Diagnosis:** *Colletes ventricarinatus* **n. sp.** is distinct in having the clypeal mid-longitudinal area depressed and lacking carina, mesosomal pubescence with off-white and black hairs intermixed, mesepisternal interspaces rugulose, T2–T5 black and covered with pale-yellow appressed hairs, and S6 carinate laterally in female.

*Colletes ventricarinatus* **n. sp.** is most similar to *C. murinus*. The female of these species, however, can be distinguished by clypeus with a transverse depression subapically in *C. ventricarinatus* **n. sp.** (clypeus with a pair of pits subapically in *C. murinus*); and S6 carinate laterally in *C. ventricarinatus* **n. sp.** (S6 not carinate laterally in *C. murinus*). The males can be differentiated by F2 1.2x as long as F1 in *C. ventricarinatus* **n. sp.** (F2 1.4x as long as F1 in *C. murinus*); and mesepisternal interspaces rugulose in *C. ventricarinatus* **n. sp.** (mesepisternal interspaces smooth in *C. murinus*).

**Description:** FEMALE (Figs. 62A, 62C, 62E):

*Dimensions (mm):* Approximate body length 10.8; head width 4.0; head length 3.0; intertegular distance 3.1; forewing length 9.2.

*Colouration:* Black except dark-brown on tegula, wing veins (except basal veins of forewing black), tibial spurs, dorsal surface of tarsomeres 3–5, marginal zones of T1–T5, ventrally reflexed lateral areas of T1. Pale-brown on marginal zones of S1–S5. Reddish-brown on distal half of tarsal claws; marked on distal 1/3 of mandible.



**Figure 62.** *Colletes ventricarinatus* Ferrari, **n. sp.** Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 2mm.

*Structure:* Labrum medially flat and without ridges. Clypeal mid-longitudinal area evenly moderately deeply depressed; depression narrow (0.5x MOD) on upper 2/3, broad (1.2x MOD) on lower 1/3; adjacent lateral area convex; apicomedial ridge absent. Malar area subequal to basal depth of mandible (25:24). F1 1.6x as long as its apical width (40:25). UID:LID (77:81). Genal area concave behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum rounded. Horizontal surface of metapostnotum ~0.6x as long as metanotum (25:44); metapostnotal pits well-delimited; posterior transverse carina sinuous and interrupted medially. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.4x longer than broad (48:14). Outer rami of hind tarsal claws ~2x as long as inner rami (17:9). Posterolateral area of S6 flat and bearing carina; marginal zone not depressed.

*Pubescence:* Mixed off-white and black, plumose, erect, long on paraocular, interantennal, frontal and genal areas (except exclusively off-white and very long near proboscidal area), pronotal lobe (except off-white hairs moderately short), mesoscutum, scutellum, mesepisternum, metepisternum, ventral surface of coxae (except moderately short), posteroventral surface of trochanters and front femur, ventral margin of mid femur; such hairs very long on vertexal area, metanotum, upper margin of lateral surface of propodeum. Fulvous, erect, moderately long setae on posterior surface of front tibia and basitarsus, dorsal surface of mid and hind tibiae and basitarsi (except suberect on mid tibia); such hairs long on posterior margin of mid basitarsus; very long on posterior margin of hind basitarsus. Fulvous, suberect, moderately short, thick setae on ventral surface of mid and hind tarsi; thickest towards distal margin. Fulvous, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T1–T5 covered with pale-yellow, dense appressed hairs (except much sparser on T1); T1 also with pale-yellow, plumose, erect, long hairs; such hairs moderately short on T2; T3–T5 also with black, erect moderately long setae (shorter on T3). S1 with pale yellow, plumose, erect, long hairs. S2 with fulvous, suberect, moderately short hairs, which are branched only apically. S3–S4 with pale-yellow, erect, moderately short setae laterally; plumose, suberect, short hairs on marginal zone. S5–S6 bare.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and finely punctate; adjacent convex area with very sparse moderately fine punctures; interspaces smooth; striate apicolaterally. Malar area longitudinally striate. Supraclypeal area rugulose but somewhat shiny. Paraocular area densely and moderately finely punctate below (except slightly coarser and

sparser towards antennal socket); punctures crowded and fine above. Frontal area densely and moderately finely punctate; interspaces rugulose. Vertexal area densely and finely punctate near lateral ocellus; sparser and with minute punctures intermingled near eye; interspaces smooth (except rugose near occipital margin). Mesoscutum and scutellum densely and moderately coarsely punctate (except moderately coarsely punctate on mesoscutal mid-posterior area); interspaces smooth. Metanotum densely and finely punctate; interspaces rugose. Mesepisternum moderately finely and moderately densely punctate; interspaces rugulose but somewhat shiny. Metepisternum rugulose above and below; obliquely striate medially. Lateral surface of propodeum with very sparse fine punctures; interspaces imbricate. Upper area of vertical surface of metapostnotum transversely striate medially. Metasomal terga minutely and moderately sparsely punctate; interspaces imbricate. Metasomal sterna finely and moderately densely punctate (except sparsely punctate on mid-longitudinal band of S2–S5 and densely punctate on mid-longitudinal band of S6).

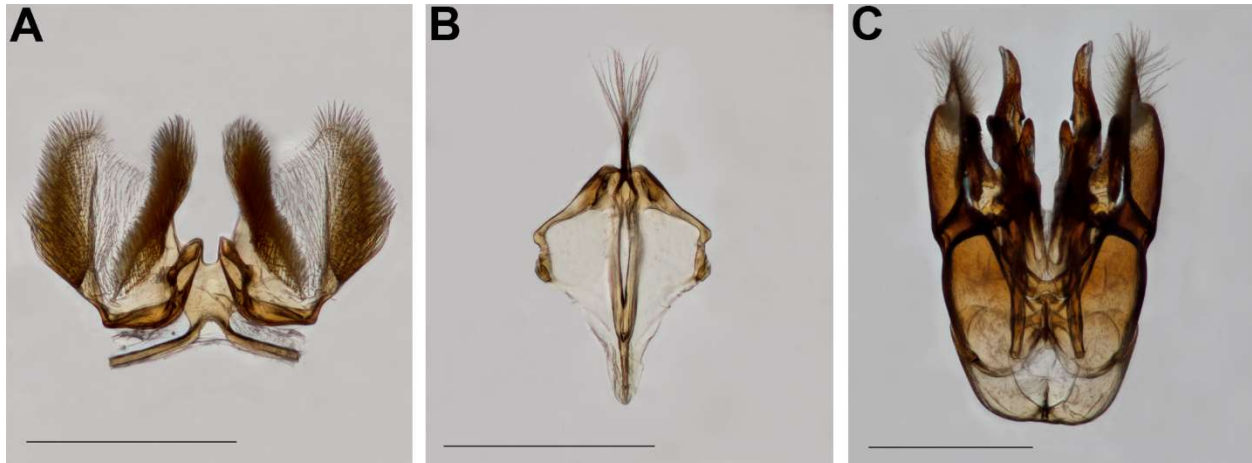
MALE (Figs. 62B, 62D, 62F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 9.3; head width 3.7; head length 2.9; intertegular distance 2.4; forewing length 8.7.

*Colouration*: Proximal half of tarsal claws pale-brown. Ventrally reflexed lateral areas of T2 and disc of S6 dark-brown.

*Structure*: Labral median area lacking ridges. Clypeal mid-longitudinal area evenly narrowly depressed (0.6x MOD). Malar area ~2x as long as basal depth of mandible (33:16). F1 1.2x as long as its apical width (27:23). UID:LID (78:72). Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.4x as long as metanotum (20:44). Hind basitarsus ~2.8x longer than broad (48:17). Outer rami of hind tarsal claws ~1.4x as long as inner rami (20:14). Posterolateral area of S6 lacking carina. S7, S8 and genital capsule as in Figs. 63A, 63B, 63C, respectively.

*Pubescence*: Setae on dorsal surface of mid basitarsus and hind basitarsus and tibia pale yellow. Pale-yellow, plumose, suberect, short hairs on marginal zones of S2–S5. Setae on S3–S4 evenly distributed. Pubescence on S5–S6 similar to that on S3–S4.



**Figure 63.** Dorsal view of the male terminalia of *C. ventricarinatus* n. sp. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Surface sculpture:* Clypeal convex area nearly impunctate. Vertexal area mostly rugose. Mesoscutal and scutellar interspaces rugulose. Upper area of vertical surface of metapostnotum transversely striate medially. S2–S6 evenly densely punctate.

**Type material:** *Holotype* ♀ – “CHILE Region I; Mirador de; Socoroma; 7.iv.00 L. Packer”. “CCDB-28231 B10”. “HOLOTYPE; *Colletes ventricarinatus* ♀; Ferrari, new species”. {PCYU}.

*Paratypes:* **CHILE – Region XV:** 2km S of Murmuntani, (-18.382, -69.549), 3340m, [L.Packer], 1♂, {PCYU}. 5km S of Putre, (-18.271, -69.573), 3548m, [L.Packer], 1♀1♂, {PCYU}. Central Hidroeléctrica de Chapiquiña, (-18.386, -69.553), 3460m, 9/iv/2000, [L.Packer], 2♀♀, {PCYU}. Mirador de Socoroma, (-18.279, -69.584), 3414m, 7/iv/2000, [L.Packer], 5♀♀, {PCYU}. Pucará Belén, (-18.472, -69.527), 3158m, 1/xi/2013, [S.Monckton], 1♂, {PCYU}. Putre, (-18.193, -69.578), 3433m, [L.Packer], 1♂, {PCYU}; idem, except 7/iv/1990, [L.Peña], 1♀, {AMNH}.

**Range:** Chile (Region XV). See also Fig. 46B.

**Biogeographic distribution:** South American transition zone (Desert and Atacama provinces). Northern Chilean species distributed in the summer rainfall area at altitudes of 3100–3600m a.s.l.

**DNA barcode:** Available. BOLD: ACK8653 (3♂♂). Distance from the nearest neighbour (*C. nigrutilus*): 7.29–7.71%.

**Floral hosts:** Unknown.

**Etymology:** The specific epithet *ventricarinatus* is a reference to the distinct carina on the lateral area of S6 in the female of this species, which is unique amongst all Chilean *Colletes*.

**Comments:** Uncommon species found only in Region XV at elevations of 3000m a.s.l. or higher.

***Colletes vicugnensis* Rojas & Toro, 1993**

(Figs. 64A–C)

*Colletes vicugnensis* Rojas & Toro, 1993: 85; Toro 1999: 31; Moure *et al.* 2007: 689; Montalva & Ruz 2010: 22; Ascher & Pickering 2017.

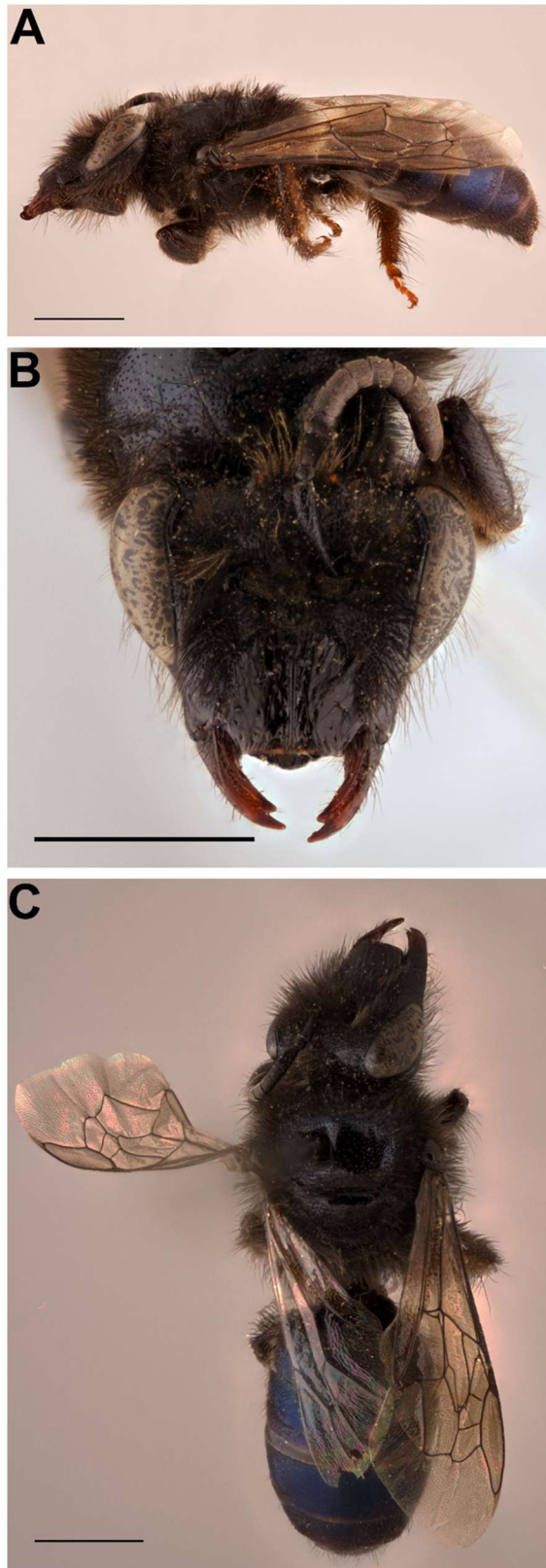
Holotype ♀ (examined). {AMNH}.

**Diagnosis:** The combination of clypeal mid-longitudinal area carinate, mesosomal pubescence black, and metasomal terga metallic blue is sufficient to differentiate the female *C. vicugnensis* (the male remains unknown) from the other Chilean species of *Colletes*, except *C. chusmiza*. However, these species can be differentiated by the facial pubescence entirely black in *C. vicugnensis* (facial pubescence with off-white and black hairs intermixed in *C. chusmiza*); ventral surface of F2–F8, mid and hind tibiae black in *C. vicugnensis* (ventral surface of F2–F8, mid and hind tibiae pale-orange in *C. chusmiza*); and the comparatively longer hind basitarsus, ~3x longer than broad, in *C. vicugnensis* (hind basitarsus ~2.5x longer than broad in *C. chusmiza*).

**Redescription:** FEMALE (Figs. 64A, 64C, 64E):

*Dimensions (mm):* Approximate body length 9.0–9.4; head width 3.0–3.1; head length 2.3; intertegular distance 2.3–2.4; forewing length 6.2–6.5.





**Figure 64.** *Colletes vicugnensis* Rojas & Toro, 1993. Female: (A) habitus, lateral view; (B) face, frontal view; (C) habitus, dorsal view. Scale bars = 2mm.

*Colouration:* Black except metallic dark-blue on T1–T5 (marginal zones of T2–T4 with purple hues). Reddish-brown on distal half of tarsal claws; marked on distal 2/3 of mandible. Dark-brown on tegula, wing veins (except vein R of forewing black), stigma, ventrally reflexed lateral areas of T1–T4, metasomal sterna (tinted with bluish reflections, except S6). Pale-brown on tibial spurs, tarsi (except posterior margin of basitarsi dark-brown), proximal half of tarsal claws.

*Structure:* Labrum medially convex; convexity not margined by ridges. Clypeal mid-longitudinal area with a strong, complete carina (except absent for upper 1/7); adjacent area declivous. Malar area ~1.3x as long as basal depth of mandible (28:22). F1 1.75x as long as its apical width (42:24). UID:LID (79:79). Genal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum triangular acute. Horizontal surface of metapostnotum ~0.4x as long as metanotum (23:56); metapostnotal pits poorly-delimited; posterior transverse carina absent. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3x longer than broad (64:21). Outer rami of hind tarsal claw 2x as long as inner rami (32:16). Posterolateral area of S6 flat and lacking carina; marginal zone not depressed.

*Pubescence:* Black, plumose, erect, long on paraocular area, lateral slopes of supraclypeal area, interantennal area, mesoscutum (except moderately short laterally), scutellum, ventral surface of mid and hind coxae, ventral margin of mid femur; such hairs very long on genal area (near proboscoidal fossa), mesepisternum, metanotum, upper margin of lateral surface of propodeum, posteroventral surface of front trochanter and femur, ventral surface of mid and hind trochanters. Interocellar area with pale-yellow hairs. Black, erect, moderately long setae on mandible, front coxa, anterior surface of front trochanter, lateral area of T4–T5; such hairs very long on posterior margin of mid and hind basitarsi. Fulvous, suberect, moderately short setae on dorsal surface of mid basitarsus and mid and hind tibiae; such setae thick on ventral surface of mid and hind tarsi (thickest towards distal margin). Black, suberect, very long hairs, which are branched only apically on anterior surface of hind femur and tibia. T1 with fulvous, plumose, suberect, moderately long hairs. Fulvous, suberect, short setae on T2–T4 and S3–S6. S1–S2 with fulvous, suberect, short hairs, which are branched only apically.

*Surface sculpture:* Clypeus shiny throughout; lateral slopes smooth; elongate punctures forming pits on lower margin and adjacently to mid-longitudinal area. Supraclypeal area

impunctate, smooth and shiny. Malar area with sparse elongate punctures. Lower paraocular area densely and moderately coarsely punctate; interspaces smooth and shiny. Upper paraocular area densely and shallowly punctate; coarser and deeper on frontal area; interspaces imbricate and dull. Vertexal area densely and moderately finely punctate (except minutely punctate besides summit of compound eye). Mesoscutum moderately finely punctate; sparsely punctate on disc; moderately densely punctate elsewhere; interspaces smooth and shiny throughout. Scutellum moderately finely and densely punctate (except impunctate on mid-longitudinal area); interspaces smooth anteriorly, imbricate medially, rugose posteriorly. Metanotum finely punctate; interspaces rugulose. Mesepisternum densely and moderately coarsely punctate; interspaces imbricate. Metepisternum obliquely striate medially; rugulose above and below. Lateral surface of propodeum minutely and sparsely punctate; interspaces imbricate. Upper area of vertical surface of metapostnotum rugose medially. Metasomal terga finely and densely punctate (except sparsely punctate on disc of T1); interspaces rugulose on disc, imbricate on marginal zone. Metasomal sterna minutely punctate (except coarser on S6); interspaces imbricate.

MALE: Unknown.

**Material studied:** *Primary type specimen:* Holotype ♀ – “HOLO; TIPO”. “CHILE, IV Región; Baños del Toro; Ene-1988; R. Solar, col.”. “Colletes; vicugnensis; Toro & Rojas 93”. “AMNH\_IZC 00324331”, {AMNH}.

*Additional specimen:* **CHILE – Region IV:** Elqui, i/1996, [Ugarte], 1 ♀, {AMNH}.

**Range:** Chile (Region IV). See also Fig. 19C.

**Biogeographic distribution:** Central Chilean sub-region (Coquimban province). Central Chilean species distributed at altitudes above 3000m a.s.l.

**DNA barcode:** Unavailable.

**Floral hosts:** Unknown.

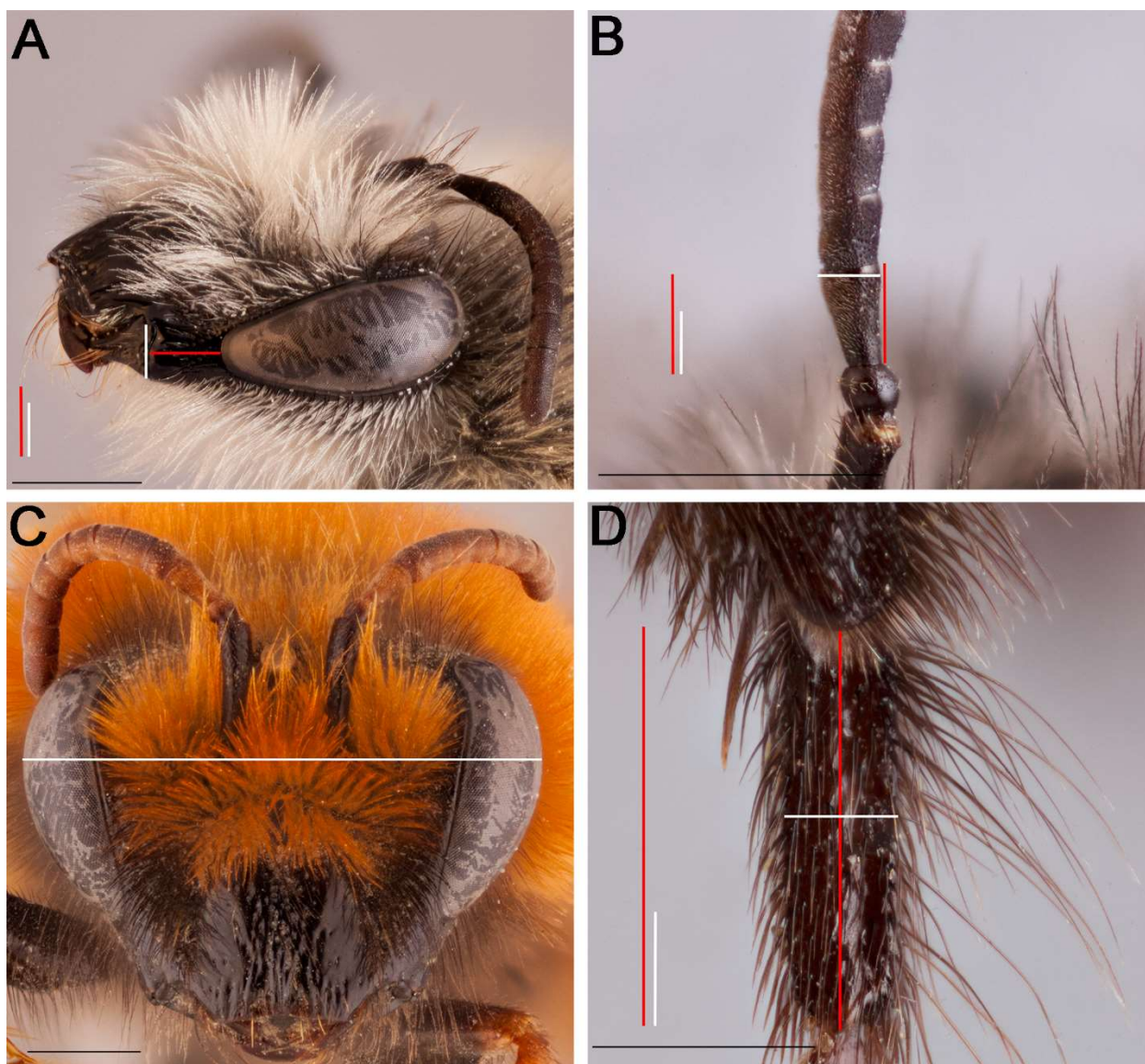
**Comments:** Extremely rare species known only from two females collected in Region IV.

### Key to the Chilean species of *Colletes*

Note 1: The males of *C. guanta*, *C. quelu* and *C. vicugnensis* are unknown.

Note 2: Refer to Figs. 65A–D to see how measurements were obtained.

1 Female .....	2
- Male .....	33
2(1) Metasoma metallic dark-blue or greenish-blue ( <i>e.g.</i> Figs. 20E, 22E, 33C) .....	3
- Metasoma black ( <i>e.g.</i> Figs. 1E, 8E, 47E) .....	11
3(2) Clypeus with a strong mid-longitudinal carina (Figs. 13C, 33B, 53B, 64B) .....	4
- Clypeus without mid-longitudinal carina ( <i>e.g.</i> Figs. 8C, 11C, 22C, 24C) .....	7
4(3) Mesoscutal pubescence black (Figs. 13A, 64A) .....	5
- Mesoscutal pubescence pale-yellow (Figs. 33A, 53A) .....	6
5(4) Facial pubescence completely black (Fig. 64B); mid and hind tibiae black (Fig. 64A); hind basitarsus 3x longer than broad .....	<i>C. vicugnensis</i> Rojas & Toro, 1993
- Facial pubescence with off-white and black hairs intermixed (Fig. 13C); mid and hind tibiae pale-orange (Fig. 13A); hind basitarsus 2.5x longer than .....	<i>C. chusmiza</i> Rojas & Toro, 1993
6(4) Malar area 1.8x as long as basal depth of mandible; F1 1.2x as long as its apical width; hind tibia dark-brown (Fig. 33A) .....	<i>C. guanta</i> Rojas & Toro, 1993
- Malar area 1.5x as long as basal depth of mandible; F1 1.4x as long as its apical width; hind tibia pale-orange (Fig. 53A) .....	<i>C. quelu</i> Rojas & Toro, 1993

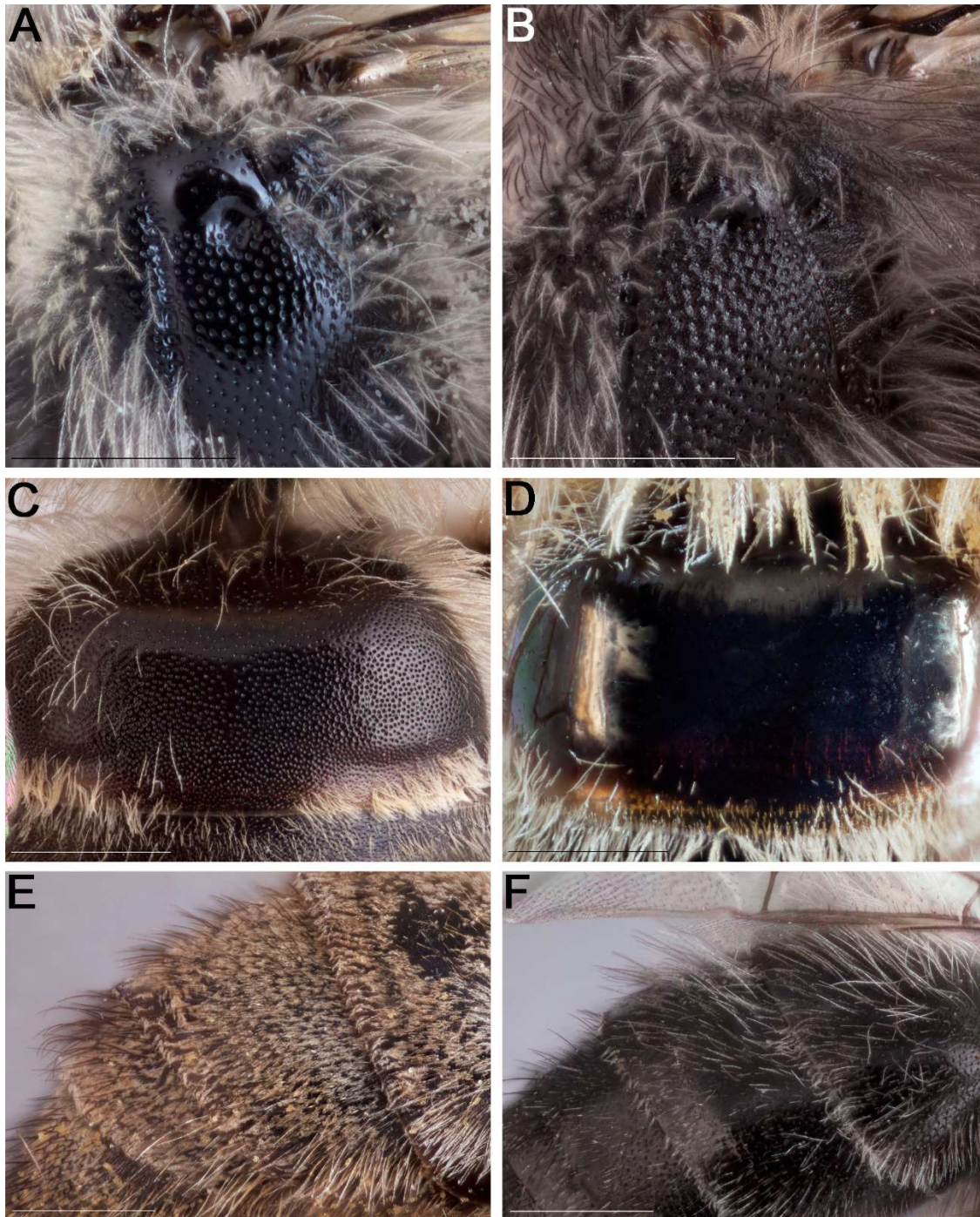


**Figure 65.** Indication on how the measurements cited in the key were obtained. (A) malar area length (red bar) and basal depth of mandible (white bar) in *Colletes kuhlmanni* n. sp.; (B) F1 length (red bar) and apical width (white bar) in *C. musculus*; (C) head width (white bar) in *C. fulvipes*; (D) hind basitarsus length (red bar) and width (white bar) in *C. bicolor*. Scale bars = 1mm.

7(3) Mesoscutal pubescence ferruginous (Fig. 11A) or pale-orange (Fig. 28A) ..... 8  
 - Mesoscutal pubescence completely black (Fig. 22A) or with off-white and black intermixed  
 (Fig. 20A) ..... 10

8(7) Facial pubescence mostly ferruginous (Fig. 28C); legs orange (Figs. 28A, 28E) .....	
..... <i>C. fulvipes</i> Spinola, 1851	
- Facial pubescence completely black (Figs. 11C, 24C); legs black (Figs. 11A, 24A) .....	9
9(8) Malar area 0.7x as long as basal depth of mandible; mesepisternum with smooth interspaces (Fig. 66A) .....	<i>C. bicolor</i> Smith, 1879
- Malar area 1.4x as long as basal depth of mandible; mesepisternum with imbricate interspaces (Fig. 66B) .....	<i>C. flaminii</i> Moure, 1956
10(7) Mesoscutal pubescence completely black (Fig. 22E); mesepisternum with smooth interspaces (Fig. 66A) .....	<i>C. cyaniventris</i> Spinola, 1851
- Mesoscutal pubescence with off-white and black hairs intermixed (Fig. 20E); mesepisternum with imbricate interspaces (Fig. 66B) .....	<i>C. cyanescens</i> (Haliday, 1836)
11(2) Malar area distinctly shorter than basal depth of mandible .....	12
- Malar area at least as long as basal depth of mandible .....	14
12(11) Mesoscutal pubescence with off-white and black hairs intermixed (Fig. 47A); metasomal terga without distal bands of appressed hairs (Fig. 47E) .....	<i>C. nigrifulus</i> Friese, 1910
- Mesoscutal pubescence ferruginous (Fig. 54A) or pale-yellow (Fig. 38A); metasomal terga with distal bands of appressed hairs (Figs. 38E, 54E) .....	13
13(12) Mesoscutal pubescence ferruginous (Fig. 54A); T1 moderately finely punctate (Fig. 66C) .....	<i>C. rutilans</i> Vachal, 1909
- Mesoscutal pubescence pale-yellow (Fig. 38A); T1 inconspicuously punctate (Fig. 66D) .....	
..... <i>C. lucens</i> Vachal, 1909	
14(11) Dorsal surface of legs with dark (fuscous or black) pubescence (Figs. 42A, 49A, 62A) .....	15
- Dorsal surface of legs with pale (off-white or pale-yellow) pubescence (e.g. Figs. 4A, 17A, 60A) .....	19

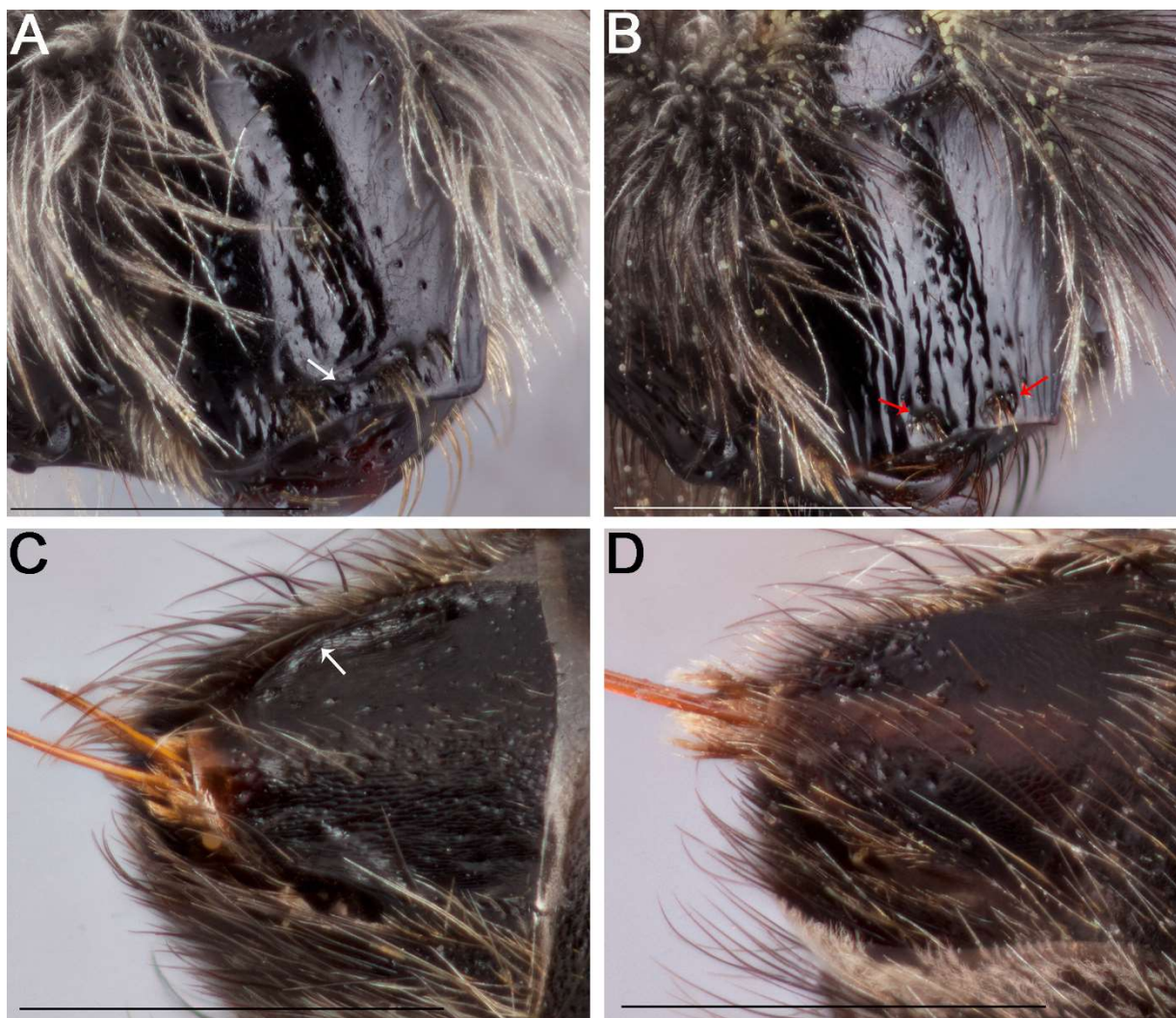




**Figure 66.** Lateral view of mesepisternum. (A) Mesepisternal interspaces smooth in the female *Colletes kuhlmanni* **n. sp.**; (B) interspaces imbricate in the female *C. cyanescens*. Dorsal view of T1. (C) T1 moderately finely punctate in the female *C. rutilans*; (D) T1 inconspicuously punctate in the female *C. lucens*. Dorsal view of T2–T5. (E) T2–T5 covered with appressed and erect hairs intermixed in the female *C. ventricarinatus* **n. sp.**; (F) T2–T5 without appressed hairs, with erect hairs only, in the female *C. alocochila*. Scale bars = 1mm.

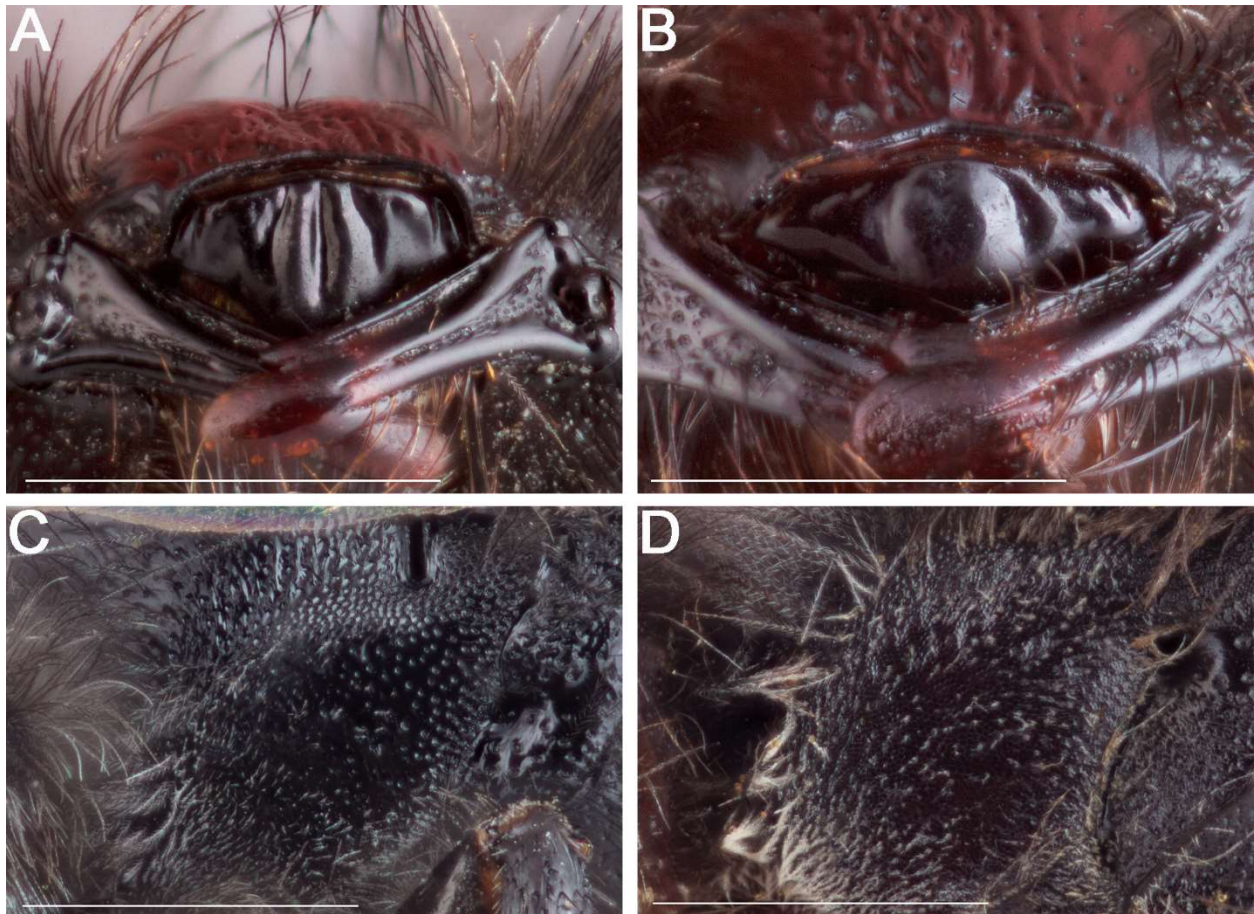
15(14) Discs of T2–T5 covered with appressed and erect hairs intermixed (Fig. 66E) .....	16
- Discs of T2–T5 without appressed hairs, with erect hairs only (Fig. 66F) .....	17
16(15) Clypeus with a transverse depression subapically (Fig. 67A); S6 carinate laterally (Fig. 67C) .....	<i>C. ventricarinatus</i> <b>n. sp.</b>
- Clypeus with a pair of pits subapically (Fig. 67B); S6 not carinate laterally (Fig. 67D) .....	<i>C. murinus</i> Friese, 1900
17(15) Mesoscutal pubescence completely black (Fig. 49A) .....	<i>C. nigropilosus</i> <b>n. sp.</b>
- Mesoscutal pubescence with off-white and black hairs intermixed (Figs. 1A, 40A) .....	18
18(17) Labrum medially concave, concavity margined by lateral ridges (Fig. 68A); lateral surface of propodeum smooth (Fig. 68C) .....	<i>C. alocochila</i> Moure, 1956
- Labrum medially convex, convexity not margined by ridges (Fig. 68B); lateral surface of propodeum imbricate (Fig. 68D) .....	<i>C. mastochila</i> Moure, 1956
19(14) Scutellar and metanotal pubescence ferruginous (Figs. 8E, 51E) .....	20
- Scutellar and metanotal pubescence off-white (Fig. 4E), pale-yellow (Fig. 6E), or with pale and dark hairs intermixed (Fig. 44E) .....	21
20(19) Head width ~4mm; mesoscutal pubescence completely ferruginous (Fig. 8E) .....	<i>C. atripes</i> Smith, 1854
- Head width ~3mm; mesoscutal pubescence mostly off-white (Fig. 51E) .....	<i>C. patagonicus</i> Schrottky, 1907
21(19) Posterior hind tibial spur pectinate (Fig. 69A) .....	22
- Posterior hind tibial spur ciliate (Fig. 69B) .....	27
22(21) Clypeus bearing mid-longitudinal ridge below (Fig. 69C) .....	23
- Clypeus without mid-longitudinal ridge below (Fig. 69D) .....	24





**Figure 67.** Oblique view of head. (A) Clypeus with a transverse depression subapically (white arrow) in the female *Colletes ventricarinatus* **n. sp.**; (B) clypeus with a pair of pits subapically (red arrows) in the female *C. murinus*. Latero-ventral view of S6. (C) S6 carinate laterally (white arrow) in the female *C. ventricarinatus* **n. sp.**; (D) S6 not carinate laterally in the female *C. murinus*. Scale bars = 1mm.

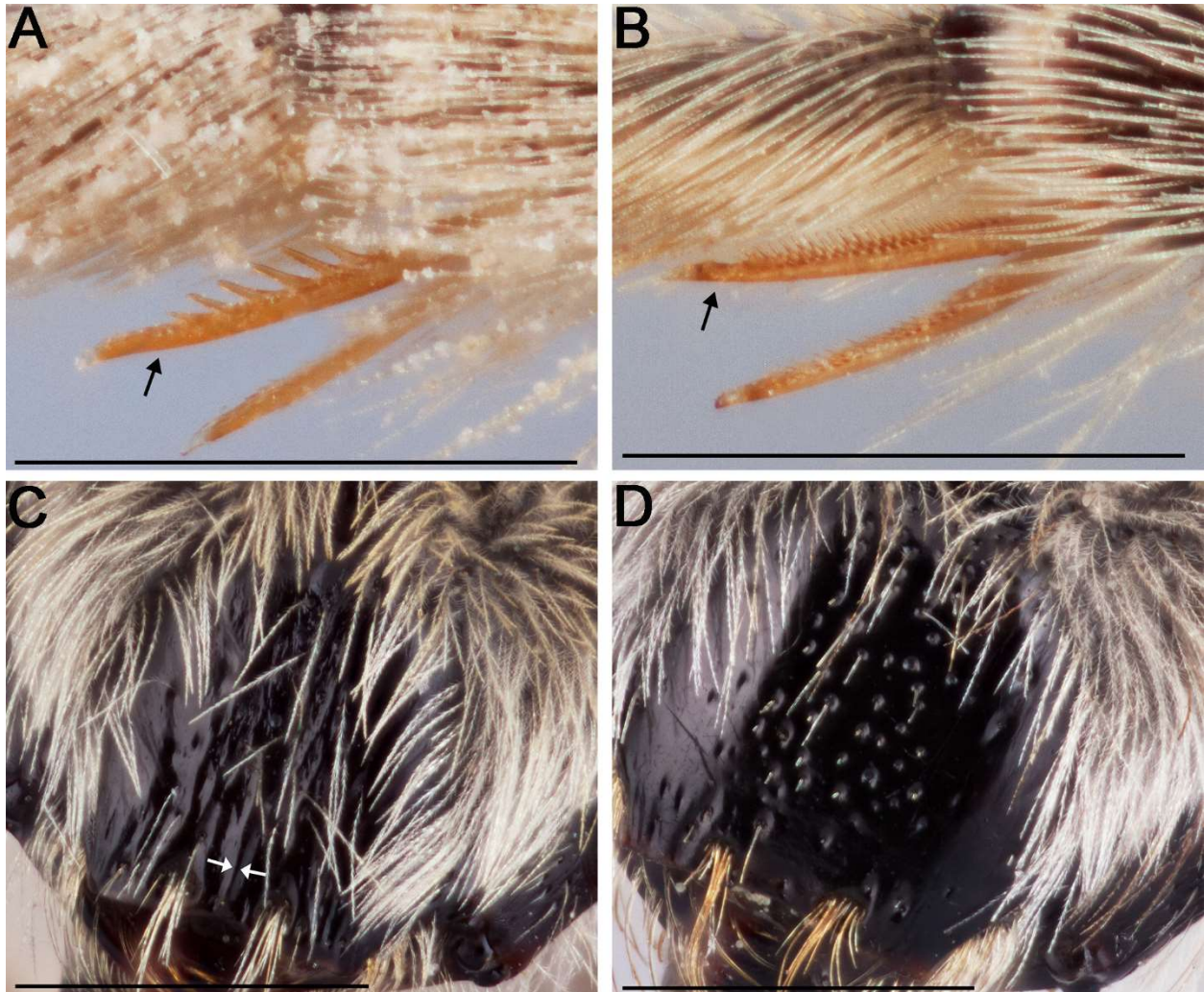
23(22) Labrum medially concave; concavity margined by lateral ridges (Fig. 68A); mesoscutal pubescence with off-white and black hairs intermixed (Fig. 17C) ..... *C. coquimbensis* **n. sp.**  
 - Labrum medially convex, convexity not margined by ridges (Fig. 68B); mesoscutal pubescence completely pale-yellow (Fig. 60C) (some slightly darker hairs may appear black when seen from some angles, therefore observing those hairs from distinct angles is advised) ..... *C. toroi* **n. sp.**



**Figure 68.** Frontal view of labrum. (A) Labrum medially concave, concavity margined by lateral ridges, in the female *Colletes alocochila*; (B) labrum medially convex, convexity not margined by ridges, in the female *C. mastochila*. Lateral view of propodeum. (C) Lateral surface of propodeum smooth in the female *C. alocochila*; (D) lateral surface of propodeum imbricate in the female *C. mastochila*. Scale bars = 1mm.

24(22) Mesepisternum with coarse and minute punctures intermingled (Fig. 70A); discs of T2–T5 not covered with appressed hairs (these are restricted to marginal zones only) (Fig. 15A) ..... *C. cognatus* Spinola, 1851  
 - Mesepisternum with moderately coarse to coarse punctures only ( Fig. 70B); discs of T2–T5 covered with pale-yellow appressed hairs (Figs. 4A, 36A) ..... 25

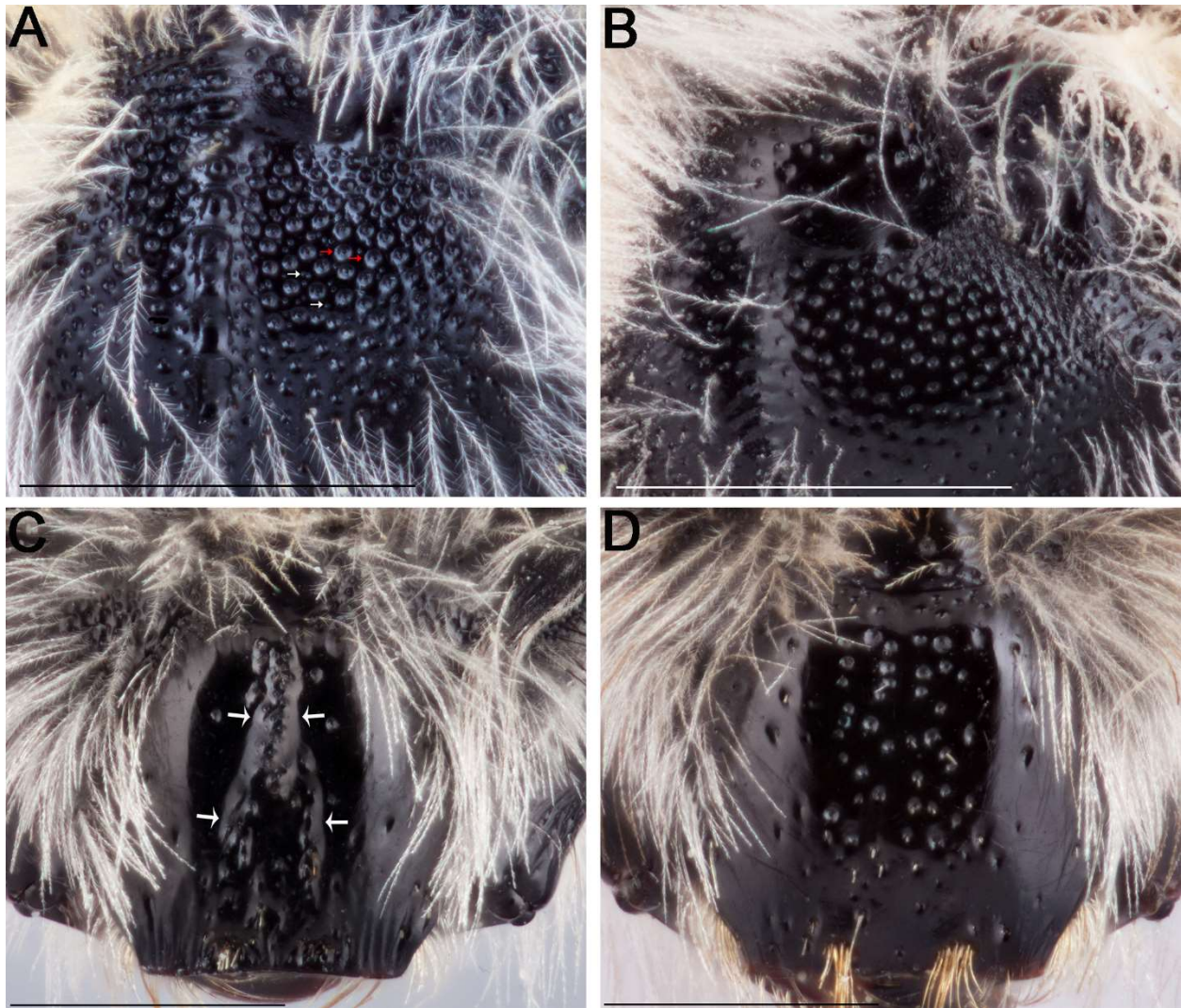




**Figure 69.** Inner view of hind leg. (A) Posterior spur pectinate (black arrow) in the female *Colletes coquimbensis* **n. sp.**; (B) spur ciliate (black arrow) in the female *C. atacamensis*. Frontal view of face. (C) Clypeus bearing mid-longitudinal ridge below in the female *C. toroi* **n. sp.** (white arrows); (D) clypeus without mid-longitudinal ridge below in the female *C. longiceps*. Scale bars = 1mm.

25(24) Paraocular area with pale-yellow and black hairs intermixed ( Figs.31A, 56A);  
mesepisternal interspaces imbricate (Fig. 66B) ..... *C. neoqueenensis* Friese, 1910  
- Paraocular area with light hairs only (Figs. 4A, 36A); mesepisternal interspaces smooth (Fig.  
66A) ..... 26

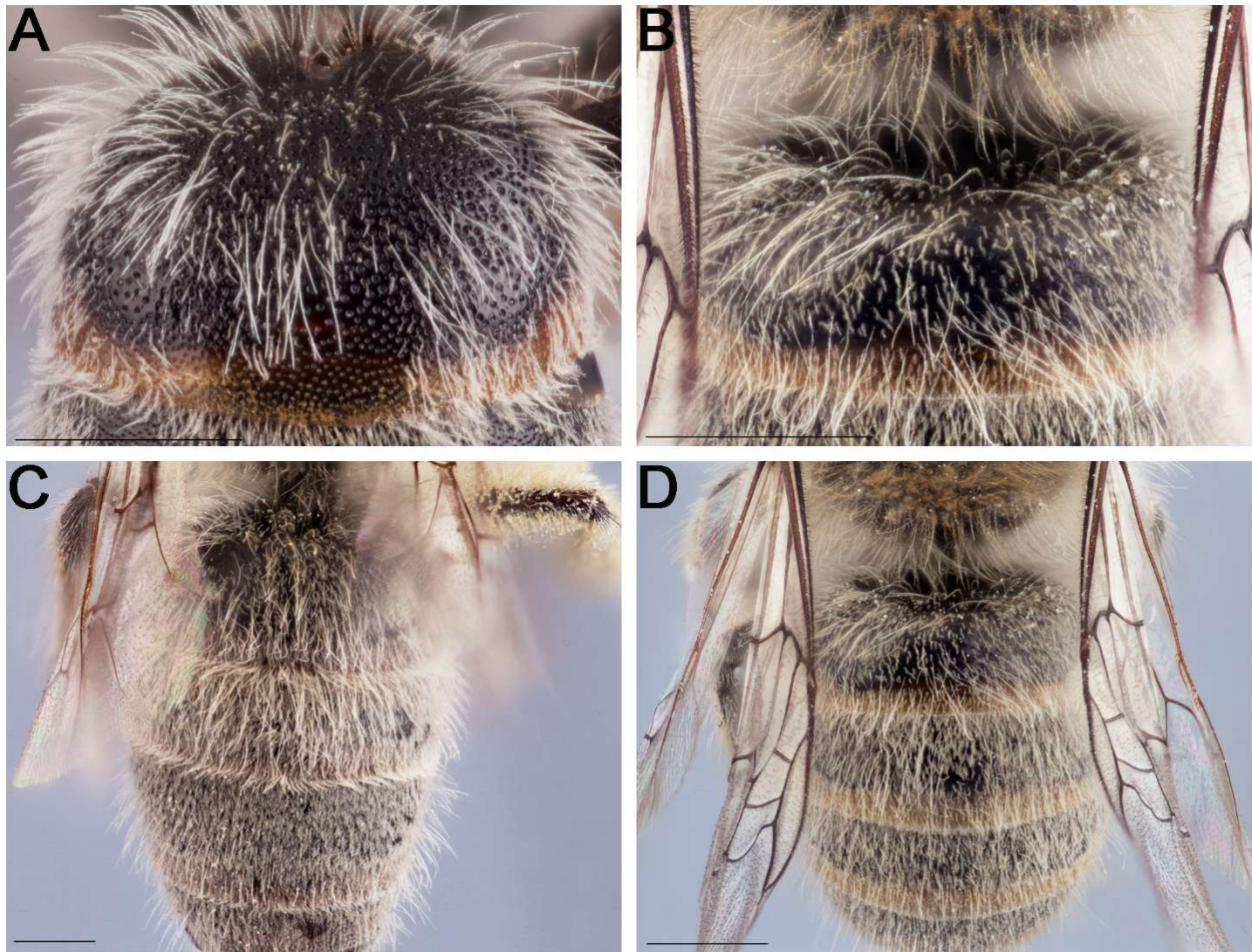




**Figure 70.** Lateral view of mesepisternum. (A) Mesepisternum with coarse (red arrows) and minute (white arrows) punctures intermingled in the female *Colletes cognatus*; (B) mesepisternum with only moderately coarse to coarse punctures in the female *C. longiceps*. Frontal view of face. (C) Clypeus depressed mid-longitudinally (white arrows) in the female *C. kuhlmanni* **n. sp.**; (D) clypeus flat mid-longitudinally in the female *C. longiceps*. Scale bars = 1mm.

26(25) Head width ~2.5mm; clypeus depressed mid-longitudinally (Fig. 70C) ... *C. arthuri* **n. sp.**  
 - Head width ~3.5mm; clypeus flat mid-longitudinally (Fig. 70D) ..... *C. longiceps* Friese, 1910



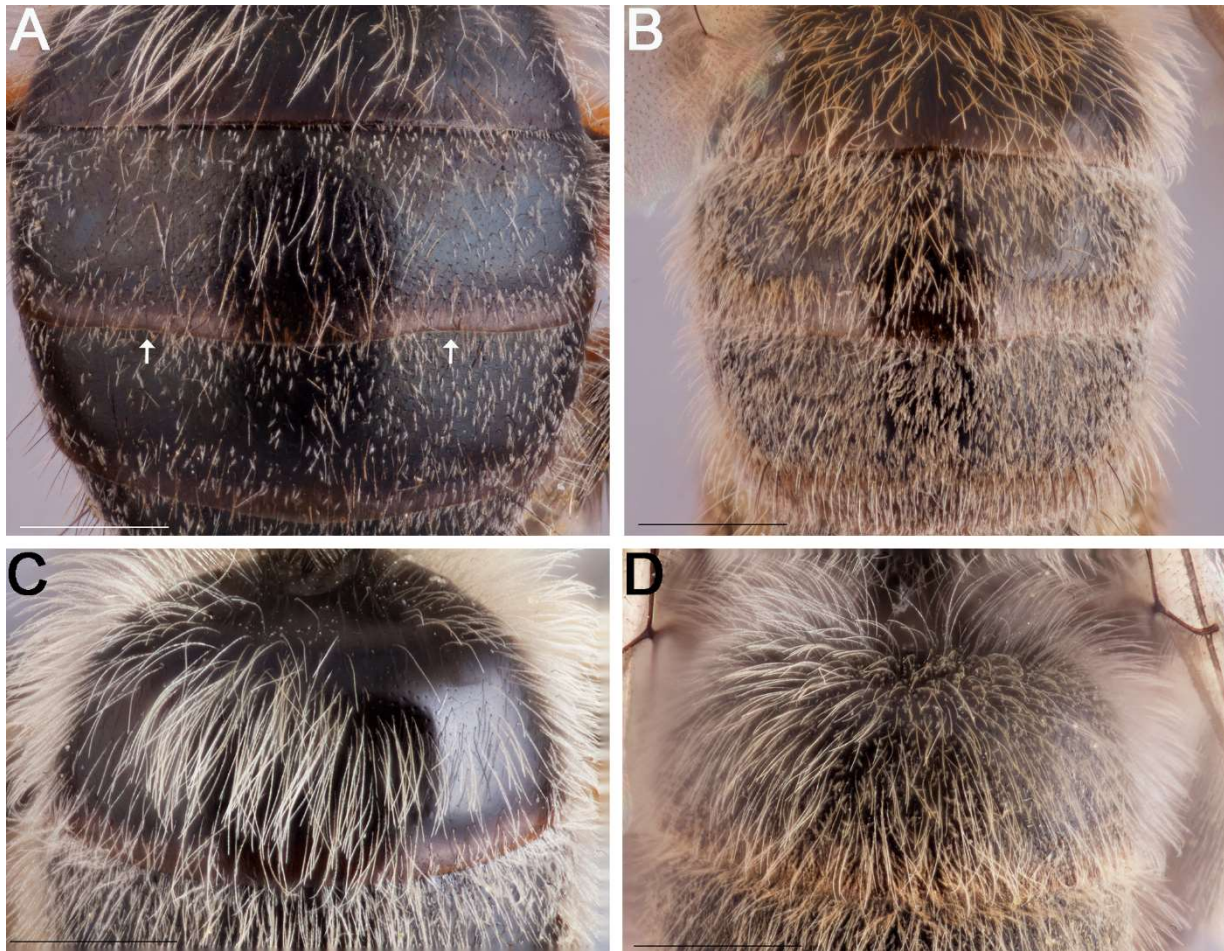


**Figure 71.** Dorsal view of metasoma. (A) T1 coarsely punctate in the female *Colletes atacamensis*; (B) T1 minutely punctate in the female *C. flavipilosus* **n. sp.**; (C) marginal zones of T1–T5 dark-brown in the female *C. sulcatus*; (D) marginal zones of T1–T5 bright-yellow in the female *C. flavipilosus* **n. sp.** Scale bars = 1mm.

- 27(21) Mesoscutal pubescence completely pale-yellow (Figs. 6A, 6E) (some slightly darker hairs may appear black when seen from some angles, therefore observing those hairs from distinct angles is advised) ..... 28
- Mesoscutal pubescence with off-white and black hairs intermixed (Figs. 44A, 44C) ..... 30
- 28(27) T1 coarsely punctate (Fig. 71A) ..... *C. atacamensis* Janvier, 1955
- T1 minutely punctate (Fig. 71B) ..... 29

29(28) Mesepisternal interspaces smooth (Fig. 66A); marginal zones of T1–T5 dark-brown to black (Fig. 71C) .....	<i>C. sulcatus</i> Vachal, 1909
- Mesepisternal interspaces imbricate (Fig. 66B); marginal zones of T1–T5 bright-yellow (Fig. 71D) .....	<i>C. flavipilosus</i> <b>n. sp.</b>
30(27) Mesepisternal interspaces imbricate (Fig. 66B); marginal zone of T2 biconvex (Fig. 72A) .....	<i>C. musculus</i> Friese, 1910
- Mesepisternal interspaces smooth (Fig. 66A); marginal zone of T2 without concavities (Fig. 72B) .....	31
31(30) T1 covered with erect hairs only (Fig. 72C) .....	<i>C. kuhlmanni</i> <b>n. sp.</b> Friese, 1910
-T1 covered with appressed and erect hairs intermixed (Fig. 72D) .....	32
32(31) Upper area of vertical surface of metapostnotum smooth (Fig. 73A); hind basitarsus about 3.5x longer than broad .....	<i>C. gilvus</i> Vachal, 1909
- Upper area of vertical surface of metapostnotum rugose (Fig. 73B); hind basitarsus about 4x longer than broad .....	<i>C. simulatus</i> <b>n. sp.</b>
33(1) Metasoma metallic dark-blue or greenish-blue ( <i>e.g.</i> Figs. 11F, 22F, 28F) .....	34
- Metasoma black ( <i>e.g.</i> Figs. 1F, 40F, 47F) .....	39
34(33) Mid and hind tarsi orange (Figs. 13B, 28B) .....	35
- Mid and hind tarsi dark-brown to black ( <i>e.g.</i> Figs. 22B, 24B) .....	36
35(34) Clypeus with a strong mid-longitudinal carina (Fig. 73C); mesoscutal pubescence with off-white and black hairs intermixed (Figs. 13B, 13D); mid and hind tibiae mostly dark-brown to black, pale-orange restricted to distal rings (Fig. 13B) .....	<i>C. chusmiza</i> Rojas & Toro, 1993
- Clypeus without mid-longitudinal carina (Fig. 73D); mesoscutal pubescence completely ferruginous (Figs. 28B, 28D); mid and hind tibiae entirely pale-orange (Fig. 28B) .....	<i>C. fulvipes</i> Spinola, 1851



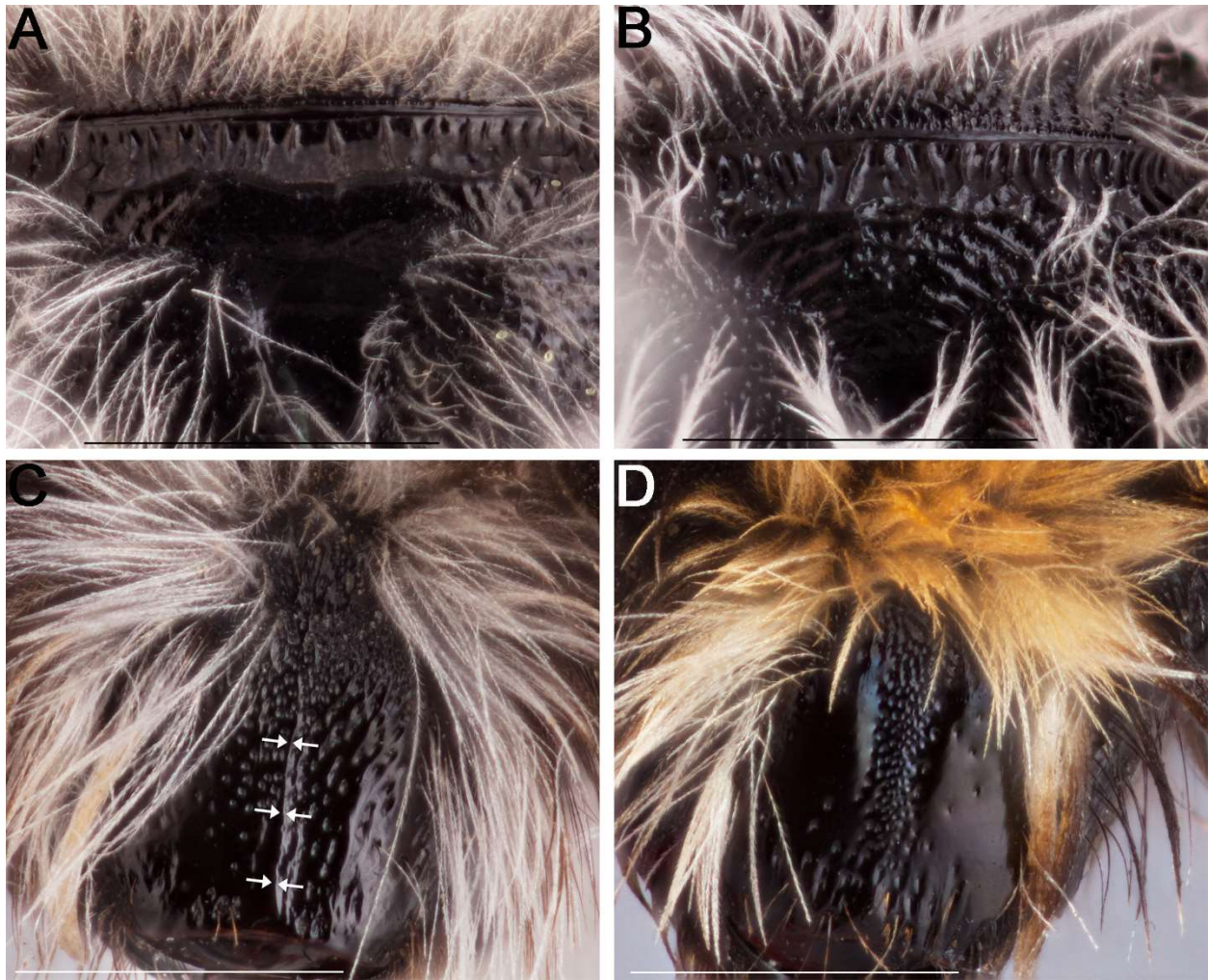


**Figure 72.** Dorsal view of metasoma. (A) Marginal zone of T2 biconvex (white arrows point to concavities) in the female *Colletes musculus*; (B) marginal zone of T2 without concavities in the female *C. kuhlmanni* **n. sp.**; (C) T1 covered with only erect hairs in the female *C. kuhlmanni* **n. sp.**; (D) T1 covered with appressed and erect hairs intermixed in the female *C. gilvus*. Scale bars = 1mm.

36(34) Mesepisternal interspaces smooth (Fig. 66A) ..... 37  
 - Mesepisternal interspaces imbricate (Fig. 66B) ..... 38

37(36) Mesoscutal pubescence ferruginous (Figs. 11B, 11D); legs with off-white to pale-yellow hairs (Fig. 11B) ..... *C. bicolor* Smith, 1879  
 - Mesoscutal pubescence with off-white and black hairs intermixed (Figs. 22B, 22D); legs with fuscous to black hairs (Fig. 22B) ..... *C. cyaniventris* Spinola, 1851



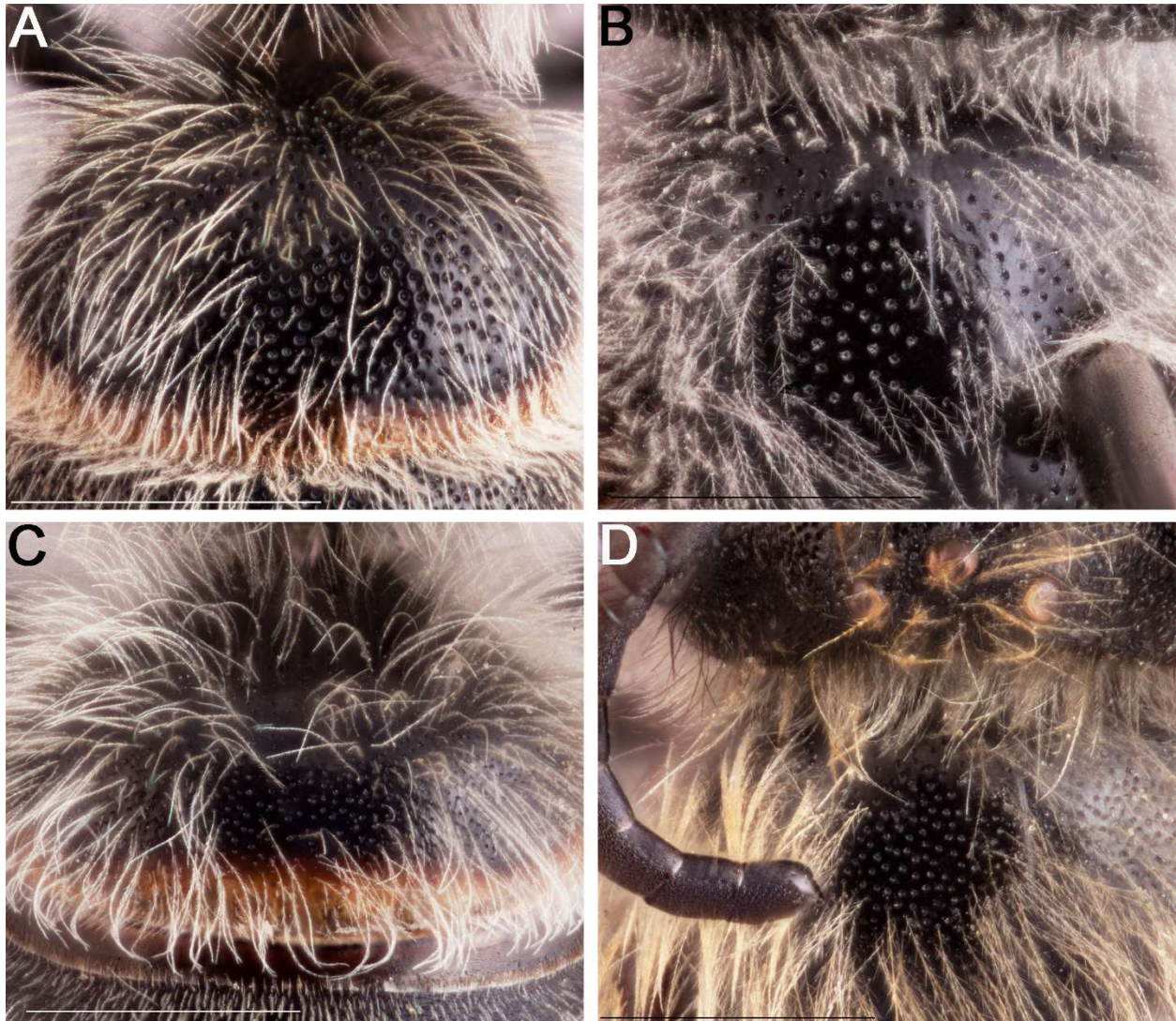


**Figure 73.** Posterior view of metapostnotum. (A) Upper area of vertical surface of metapostnotum smooth in the female *Colletes gilvus*; (B) upper area rugose in the female *C. simulatus* **n. sp.** Frontal view of head. (C) Clypeus with a mid-longitudinal carina (white arrows) in the male *C. chusmiza*; (D) clypeus without mid-longitudinal carina in the male *C. fulvipes*. Scale bars = 1mm.

38(36) Malar area about 1.5x as long as basal depth of mandible; mesoscutal pubescence pale-yellow to ferruginous (Figs. 24B, 24F) ..... *C. flaminii* Moure, 1956  
 - Malar area about 2x as long as basal depth of mandible; mesoscutal pubescence with off-white and black hairs intermixed (Figs. 20B, 20F) ..... *C. cyanescens* (Haliday, 1836)

39(33) Malar area short, at most, as long as basal depth of mandible .....	40
- Malar area long, at least, 1.5x as long as basal depth of mandible .....	42
40(39) Mesoscutal pubescence with off-white and black hairs intermixed (Figs. 47B, 47D); metasomal terga without distal bands of appressed hairs (Fig. 47F) .....	<i>C. nigrutilus</i> Friese, 1900
- Mesoscutal pubescence pale-yellow (Figs. 38B, 38D) or ferruginous (Figs. 54B, 54D); metasomal terga with distal bands of appressed hairs (Fig. 38F) .....	41
41(40) Malar area about 0.7x as long as basal depth of mandible; mesoscutal pubescence pale- yellow (Figs. 38B, 38D); T1 minutely punctate (Fig. 66D) .....	<i>C. lucens</i> Vachal, 1909
- Malar area about 0.9x as long as basal depth of mandible; mesoscutal pubescence ferruginous (Figs. 54B, 54D); T1 moderately finely punctate (Fig. 66C) .....	<i>C. rutilans</i> Vachal, 1909
42(39) Punctures on T1 (Fig. 74A) as coarse as or coarser than those of mesoscutum (Fig. 74B) .....	43
- Punctures on T1 (Fig. 74C) finer than those of mesoscutum (Fig. 74D) .....	44
43(42) Paraocular pubescence completely off-white (Fig. 6B) (some slightly darker hairs may appear black when seen from some angles, therefore observing those hairs from distinct angles is advised); mesoscutum moderately sparsely punctate (i= 1.5–2d) anteriorly (Fig. 74B) .....	<i>C. atacamensis</i> Janvier, 1955
- Paraocular pubescence with off-white and black hairs intermixed (Fig. 56B); mesoscutum densely punctate (i= 0.5–1d) anteriorly (Fig. 74D) .....	<i>C. simulatus</i> <b>n. sp.</b>
44(42) Mesepisternal interspaces imbricate (Fig. 66B) .....	45
- Mesepisternal interspaces smooth (Fig. 66A) .....	50
45(44) Mesoscutal pubescence completely pale-yellow (Figs. 26D, 36D) (some slightly darker hairs may appear black when seen from some angles, therefore observing those hairs from distinct angles is advised) .....	46
- Mesoscutal pubescence with off-white and black hairs intermixed (Figs. 44D, 62D) .....	48





**Figure 74.** Dorsal view of mesosoma and metasoma of the male *Colletes atacamensis*. (A) Punctures on T1 coarser than (B) those of mesoscutum. Dorsal view of mesosoma and metasoma of the male *C. flavipilosus* n. sp. (C) Punctures on T1 finer than (D) those of mesoscutum. Scale bars = 1mm.

46(45) Scutellar and metanotal pubescence ferruginous, strongly contrasting with the pale-yellow hairs on mesoscutum (Fig. 51F) ..... *C. patagonicus* Schrottky, 1907  
 - Scutellar and metanotal pubescence pale-yellow, the same colour as on mesoscutum (Figs. 26F, 36F) ..... 47



- 47(46) Paraocular pubescence completely pale-yellow (Fig. 36B) (some slightly darker hairs may appear black when seen from some angles, therefore observing those hairs from distinct angles is advised); F3–F8 ~1.7x as long as wide ..... *C. longiceps* Friese, 1910  
- Paraocular pubescence with pale-yellow and black hairs intermixed (Fig. 26B); F3–F8 ~1.2x as long as wide ..... *C. flavipilosus* **n. sp.**
- 48(45) Supraclypeal area smooth (Fig. 75A); mid and hind tibiae and tarsi with black setae (Fig. 40B) ..... *C. mastochila* Moure, 1956  
- Supraclypeal area rugulose or imbricate (Fig. 75B); mid and hind tibiae and tarsi with pale-yellow setae (Figs. 44B, 62B) ..... 49
- 49(48) Disc of T2 covered with appressed and erect hairs intermixed (Fig. 66E); marginal zone of T2 without concavities (Fig. 72B) ..... *C. ventricarinatus* **n. sp.**  
- Disc of T2 without appressed hairs, with erect hairs only (Fig. 66F); marginal zone of T2 biconvex (Fig. 72A) ..... *C. musculus* Friese, 1910
- 50(44) Mesoscutal pubescence with off-white and black hairs intermixed (*e.g.* Figs. 1D, 31D) ..... 51  
- Mesoscutal pubescence completely pale-yellow (Fig. 4D), bright-yellow (Fig. 15D) or ferruginous (Fig. 8D) ..... 54
- 51(50) Upper margin of lateral surface of propodeum with pale-yellow pubescence (Fig. 75C); T2–T5 with well-defined distal bands of appressed hairs (Fig. 31B) ..... *C. gilvus* Vachal, 1909  
- Upper margin of lateral surface of propodeum with black pubescence (Fig. 75D); T2–T5 without distal bands of appressed hairs (*e.g.* Figs. 1B, 49B) ..... 52
- 52(51) Legs with black hairs (Fig. 49B) ..... *C. nigropilosus* **n. sp.**  
- Legs with off-white or pale-yellow hairs (Figs. 1B, 42B) ..... 53



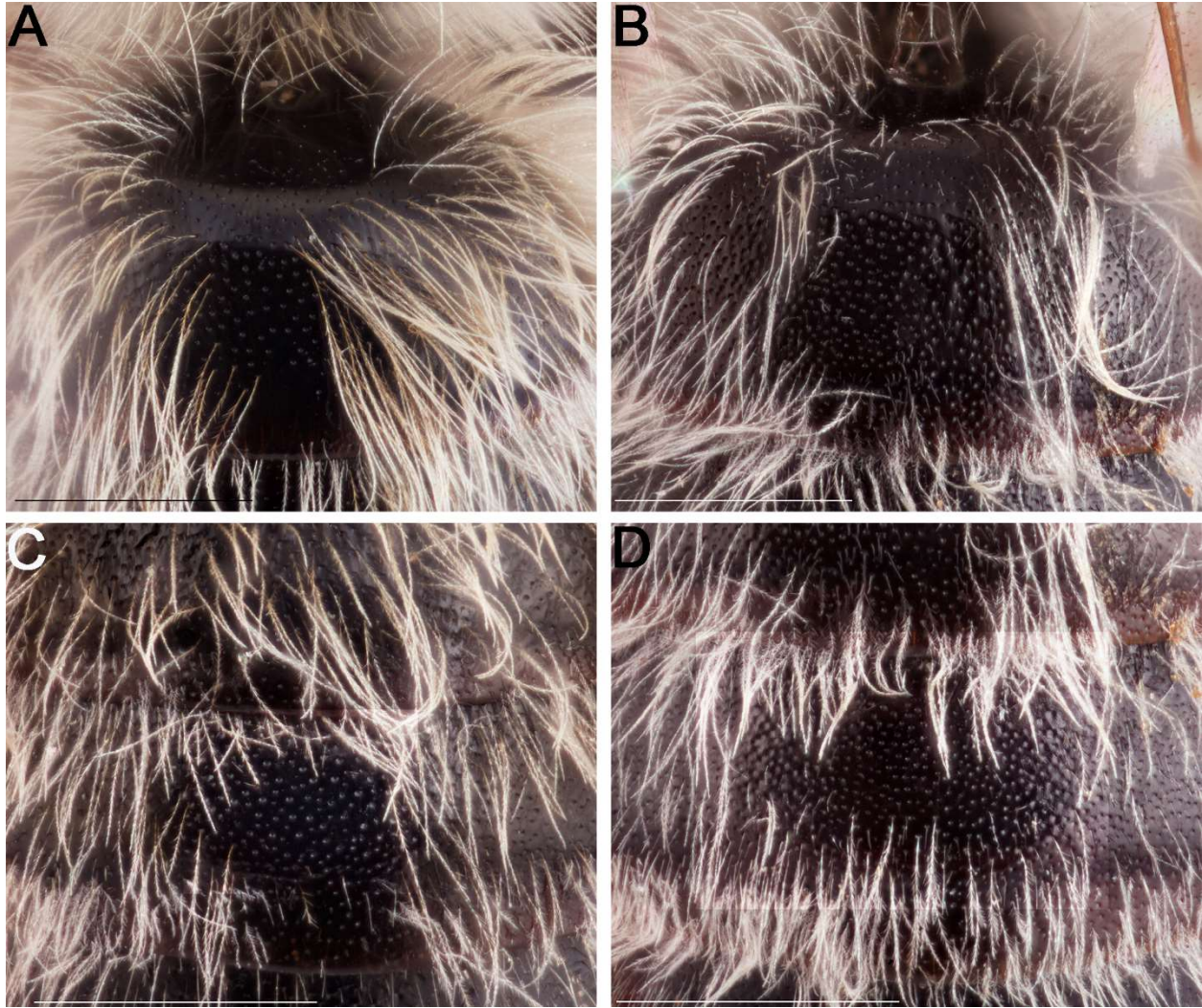
**Figure 75.** Frontal view of head. (A) Supraclypeal area smooth in the male *Colletes mastochila*; (B) supraclypeal area imbricate in the male *C. ventricarinatus* n. sp. Lateral view of propodeum. (C) Upper margin with pale-yellow pubescence (black dashed-line ellipse) in the male *C. gilvus*; (D) upper margin with black pubescence (white dashed-line ellipse) in the male *C. murinus*.

Scale bars = 1mm.

53(52) F1 as long as its apical width; discs of T2–T5 covered with appressed and erect hairs intermixed (Fig. 66E) ..... *C. murinus* Friese, 1900  
 - F1 about 1.2x as long as its apical width; discs of T2–T5 without appressed hairs, with erect hairs only (Fig. 66F) ..... *C. alocochila* Moure, 1956

54(50) Paraocular pubescence completely pale (Figs. 4B, 15B) (some slightly darker hairs may appear black when seen from some angles, therefore observing those hairs from distinct angles is advised) .....	55
- Paraocular pubescence with off-white and black hairs intermixed (e.g. Figs. 34B, 58B) .....	56
55(54) Malar area ~1.5x as long as basal depth of mandible; mesepisternum with coarse and minute punctures intermingled (Fig. 70A) .....	<i>C. cognatus</i> Spinola, 1851
- Malar area ~2x as long as basal depth of mandible; mesepisternum with moderately coarse punctures only (Fig. 70B) .....	<i>C. arthuri</i> <b>n. sp.</b>
56(54) Mesoscutum and T1 with ferruginous or pale-orange pubescence (Fig. 8F); T2–T5 without distal bands of appressed hairs (Fig. 8F) .....	<i>C. atripes</i> Smith, 1854
- Mesoscutum and T1 with pale-yellow pubescence (e.g. Figs. 17F, 60F); T2–T5 with well-defined distal bands of appressed hairs (e.g. Fig. 15F, 38F) .....	57
57(56) Malar area about 1.5x as long as basal depth of mandible .....	<i>C. coquimbensis</i> <b>n. sp.</b>
- Malar area at least 2x as long as basal depth of mandible .....	58
58(57) T1 sparsely (i= 2–3d) punctate medially (Fig. 76A) .....	<i>C. kuhlmanni</i> <b>n. sp.</b> Friese, 1910
- T1 densely (i= 0.5–1d) punctate medially (Fig. 76B) .....	59
59(58) Hind basitarsus about 4.5x longer than broad; T2 moderately densely (i= 1–1.5d) punctate medially (Fig. 76C) .....	<i>C. sulcatus</i> Vachal, 1909
- Hind basitarsus about 3.5x longer than broad; T2 densely (i= 0.5–1d) punctate medially (Fig. 76D) .....	<i>C. toroi</i> <b>n. sp.</b>





**Figure 76.** Dorsal view of metasoma. (A) T1 sparsely punctate medially in the male *Colletes kuhlmanni* n. sp.; (B) T1 densely punctate medially in the male *C. toroi* n. sp.; (C) T2 moderately densely punctate medially in the male *C. sulcatus*; (D) T2 densely punctate medially in the male *C. toroi* n. sp. Scale bars = 1mm.

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## Appendix I: Supplementary tables

**Table S1.** List of the barcoded *Colletes* specimens.

Species	Locality	Sex	BOLD sample ID	BOLD BIN
<i>Colletes alocochila</i>	Chile, Region XV, NE of Putre	♀	CCDB-22014-A09	BOLD: ACW1920
	Chile, Region XV, NE of Putre	♀	CCDB-22014-E12	BOLD: ACW1921
	Chile, Region I, Highway 687 km 83	♀	CCDB-22014-A11	BOLD: ACW1920
	Chile, Region I, Highway 687 km 83	♂	CCDB-22014-C03	BOLD: ACW1920
	Chile, Region I, Highway 687 km83	♀	CCDB-22014-E10	BOLD: ACW1920
	Chile, Region I, Highway 687 km 83	♀	CCDB-22014-F02	BOLD: ACW1920
	Chile, Region I, Highway 687 km 83	♀	CCDB-28231-B04	BOLD: ACW1920
	Chile Region II, Road to Machuca	♂	CCDB-22014-C05	BOLD: ACW1920
<i>C. arthuri</i> n. sp.	Chile, Region I, 71km E of Pozo Almonte	♀	CCDB-22009-H03	BOLD: AAN4840
	Chile, Region I, 71km E of Pozo Almonte	♀	CCDB-22015-B09	BOLD: AAN4840
	Chile, Region I, 73km E of Pozo Almonte	♀	CCDB-22009-H01	BOLD: AAN4840
	Chile, Region I, 73km E of Pozo Almonte	♀	CCDB-22009-H02	BOLD: AAN4840
	Chile, Region I, 73km E of Pozo Almonte	♀	CCDB-22009-H09	BOLD: AAN4840
	Chile, Region I, 73km E of Pozo Almonte	♀	CCDB-22009-H10	BOLD: AAN4840
	Chile, Region I, 73km E of Pozo Almonte	♂	CCDB-22015-B01	BOLD: AAN4840
	Chile, Region I, 73km E of Pozo Almonte	♂	CCDB-22015-B03	BOLD: AAN4840
	Chile, Region I, 73km E of Pozo Almonte	♂	CCDB-15274-D05	BOLD: AAN4840
	Chile, Region I, 79.8km ESE of Pozo Almonte	♀	3770G01-CHL	BOLD: AAN4840
	Chile, Region II, 5–7km E of Aguas Blancas	♀	CCDB-09984-B05	BOLD: AAN4840
	Chile, Region II, Talabre	♀	CCDB-10037-A06	BOLD: AAN4840
<i>C. atacamensis</i>	Chile, Region I, 10km E of Pozo Almonte	♀	CCDB-09984-A06	BOLD: AAJ6725
	Chile, Region I, 23km E of Pozo Almonte	♂	CCDB-22014-G02	BOLD: AAJ6725
	Chile, Region I, 23km E of Pozo Almonte	♀	CCDB-22014-G04	BOLD: AAJ6725
	Chile, Region I, 23km E of Pozo Almonte	♂	CCDB-22014-G06	BOLD: AAJ6725
	Chile, Region I, E of Pozo Almonte	♂	CCDB-22015-C03	BOLD: AAJ6725
	Chile, Region I, Pozo Almonte	♂	CCDB-28315-B02	BOLD: AAJ6725

<i>C. atripes</i>	Chile, Region I, Highway A-65 km 37	♂	CCDB-22014-D04	BOLD: AAJ6725
	Chile, Region I, Yala-yala	♀	CCDB-09981-D12	BOLD: AAJ6725
	Chile, Region II, Aguas Blancas	♂	CCDB-22015-D01	BOLD: AAJ6725
	Chile, Region II, 16km N of Taltal	♀	CCDB-09981-H07	BOLD: ACF5893
	Chile, Region III, 8km W Domeyko	♂	CCDB-28312-H08	BOLD: AAF4094
	Chile, Region III, 16km of Copiapó bypass	♂	CCDB-09858-B04	BOLD: AAF4094
	Chile, Region III, Caldeira	♀	CCDB-22009-E08	BOLD: AAF4094
	Chile, Region III, Caleta Chañaral de Aceituna	♂	CCDB-10006-C02	BOLD: ACF5893
	Chile, Region III, E of Chañaral	♂	CCDB-10006-H05	BOLD: ACF5893
	Chile, Region III, Highway 5 km 848	♀	06729B01-CHL	BOLD: ACF5893
	Chile, Region III, NE of Aguada de Tongoy	♀	CCDB-09866-H02	BOLD: ACF5893
	Chile, Region III, NE of Aguada de Tongoy	♂	CCDB-09866-H01	BOLD: AAF4094
	Chile, Region III, NW of Copiapó	♀	CCDB-09981-H08	BOLD: ACF5893
	Chile, Region IV, Los Choros	♂	CCDB-09866-H09	BOLD: AAF4094
	Chile, Region IV, Parque Nacional Fray Jorge	♀	CCDB-09981-H06	BOLD: ACF5893
	Chile, Region IV, S of Vicuña	♀	CCDB-22009-E09	BOLD: AAF4094
<i>C. bicolor</i>	Argentina, Catamarca, 5km NE of Santa Maria	♀	CCDB-15259-B04	BOLD: AAF4093
	Chile, Region III, 1km N of Caldera	♂	B03750F05-CHL	BOLD: AAJ6724
	Chile, Region III, Pesquera Bahía Caldera	♀	CCDB-28237-A05	BOLD: AAJ6724
<i>C. chusmiza</i>	Chile, Region I, Highway 687 km 83	♀	CCDB-22014-C01	BOLD: ACW1705
	Chile, Region I, Highway 687 km 83	♂	CCDB-22014-B11	BOLD: ACW1705
<i>C. cognatus</i>	Argentina, Chubut, Trevelin	♂	ARG-14508-12	BOLD: ABA0478
	Argentina, Chubut, Trevelin	♂	ARG-14508-54	BOLD: ABA0478
	Argentina, Chubut, Trevelin	♂	ARG-14508-55	BOLD: ABA0478
	Argentina, Chubut, Trevelin	♂	ARG-14508-11	BOLD: ABA0479
	Argentina, Chubut, Trevelin	♂	ARG-14508-53	BOLD: ABA0479
	Chile, Region IV, 7km N of Los Vilos	♂	CCDB-28231-A09	BOLD: ABA0478
<i>C. coquimbensis</i> n. sp.	Chile, Region IV, La Mercedes	♀	CCDB-10006-B12	BOLD: AAO3472
	Chile, Region IV, La Mercedes	♀	CCDB-09866-C03	BOLD: AAO3472
	Chile, Region IV, Las Placetas	♂	CCDB-28315-E02	BOLD: AAO3472
	Chile, Region IV, Las Placetas	♂	CCDB-28237-F04	BOLD: AAO3472
<i>C. cyanescens</i>	Argentina, Chubut, 8km N of Sarmiento	♀	CCDB-15259-C06	BOLD: ABY2997



	Argentina, Chubut, Loma del Medio	♂	CCDB-15259-B07	BOLD: ABY2997
	Argentina, Chubut, Trevelin	♀	ARG-14508-05	BOLD: ABY2997
	Argentina, Chubut, Trevelin	♂	ARG-14508-06	BOLD: ABY2997
	Argentina, Chubut, Trevelin	♂	ARG-14508-07	BOLD: ABY2997
	Argentina, Chubut, Trevelin	♂	ARG-14490-24	BOLD: ABY2997
	Argentina, Chubut, Trevelin	♂	1406-C10	BOLD: ABY2997
	Argentina, Chubut, Trevelin	♀	1399-C10	BOLD: ABY2997
	Argentina, Santa Cruz, 0.5km E of Los Antiguos	♀	CCDB-15259-C04	BOLD: ABY2997
	Argentina, Santa Cruz, 0.5km E of Los Antiguos	♂	CCDB-15259-C05	BOLD: ABY2997
	Argentina, Santa Cruz, 0.5km E of Los Antiguos	♀	CCDB-06743-D12	BOLD: ABY2997
	Chile, Region III, Highway C-13 km 15	♂	CND-06715-60	BOLD: ABY2997
	Chile, Region III, Highway C-13 km 15	♂	CND-06715-61	BOLD: ABY2997
	Chile, Region III, Highway C-13 km 15	♂	CND-06715-62	BOLD: ABY2997
	Chile, Region III, Highway C-13 km 15	♂	CND-06715-63	BOLD: ABY2997
	Chile, Region III, Highway C-13 km 15	♂	CND-06715-64	BOLD: ABY2997
	Chile, Region III, Highway C-13 km 15	♂	CND-06715-65	BOLD: ABY2997
	Chile, Region IV, La Mercedes	♀	CCDB-09866-C04	BOLD: ABY2997
	Chile, Region IV, Los Vilos	♀	CCDB-09858-F04	BOLD: ABY2997
	Chile, Region IV, N of Los Hornos	♀	1399-D04	BOLD: AAC8707
	Chile, Region IV, N of Los Hornos	♀	1406-D04	BOLD: ABY2997
	Chile, Region Metropolitana, Caleu	♂	CCDB-09857-B04	BOLD: ABY2997
	Chile, Region IX, Parque Nacional Nahuelbuta	♀	CCDB-03755-E04	BOLD: AAC8707
	Chile, Region IX, Parque Nacional Nahuelbuta	♀	1406-D03	BOLD: ACW1675
<i>C. cyaniventris</i>	Chile, Region VII, E of Lago Colbun	♀	CCDB-09984-A09	BOLD: AAV8114
<i>C. flaminii</i>	Argentina, Santa Cruz, 25km E of Los Antiguos	♀	CCDB-22015-B11	BOLD: AAO3445
	Chile, Region VII, W of Laguna del Maule	♀	CCDB-10006-D07	BOLD: AAO3445
	Chile, Region IX, Río Liucura	♂	CCDB-28237-E05	BOLD: AAO3445
<i>C. flavipilosus n. sp.</i>	Chile, Region V, Portillo	♂	CCDB-22015-B05	BOLD: AAO3408
	Chile, Region VII, Laguna del Maule	♀	CCDB-22009-H04	BOLD: ACV1795
	Chile, Region VII, Laguna del Maule	♂	CCDB-09858-D09	BOLD: AAO3408
	Chile, Region VII, Laguna del Maule	♂	CCDB-22009-H05	BOLD: AAO3408
	Chile, Region VII, Laguna del Teno	♀	CCDB-28313-F09	BOLD: AAO3408

<i>C. fulvipes</i>	Chile, Region VII, Laguna del Maule	♀	CCDB-22009-F10	BOLD: AAO3473
	Chile, Region VII, Laguna del Maule	♀	CCDB-10006-D10	BOLD: AAO3473
	Chile, Region VIII, Termas de Chillán	♀	CCDB-22009-F09	BOLD: AAO3473
	Chile, Region IX, Questa las Raices	♂	CCDB-19991-B04	BOLD: AAO3473
<i>C. gilvus</i>	Chile, Region XV, Quebrada Cardones	♀	CCDB-22015-D11	BOLD: AAJ7575
	Chile, Region XV, Zapahuira	♂	CCDB-22009-G11	BOLD: AAJ7575
	Chile, Region XV, Zapahuira	♂	CCDB-22009-G12	BOLD: AAJ7575
	Chile, Region I, Estación Regadio	♀	CCDB-09984-B01	BOLD: AAJ7575
	Chile, Region I, Pampa Oxaya	♂	CCDB-22015-E10	BOLD: AAJ7575
	Chile, Region I, S of Putre	♀	CCDB-09984-B02	BOLD: AAJ7575
	Chile, Region I, Usmagama	♀	CCDB-09981-H09	BOLD: AAJ7575
	Chile, Region II, Highway 23 km 175	♀	CCDB-09981-H10	BOLD: AAJ7575
	Chile, Region II, Road to Machuca km 5.4	♂	CCDB-22014-C09	BOLD: AAJ7575
	Chile, Region II, Talabre	♀	CCDB-10037-A04	BOLD: AAJ7575
	Chile, Region II, Talabre	♀	CCDB-10037-A05	BOLD: AAJ7575
<i>C. kuhlmanni</i> n. sp.	Chile, Region III, N of Vallenar	♂	CCDB-09981-D03	BOLD: AAO3265
	Chile, Region III, NE Aguada de Tongoy	♂	CCDB-09866-G10	BOLD: AAO3265
	Chile, Region III, Puente Rio Potro	♂	CCD-B10006-E12	BOLD: AAO3265
	Chile, Region III, Quebrada del Potrero	♂	CCDB-09858-E12	BOLD: AAO3265
	Chile, Region III, S of Chachiyuyo	♂	CCDB-10006-E07	BOLD: AAO3265
	Chile, Region III, S of Freirina	♂	CCDB-09866-E02	BOLD: AAO3265
	Chile, Region V, E of Rio Blanco	♀	CCDB-10006-B11	BOLD: AAO3265
	Chile, Region Metropolitana, Cerro El Roble	♀	CCDB-10006-C03	BOLD: AAO3265
	Chile, Region Metropolitana, Cuna Gallego Valley	♀	CCDB-22014-B03	BOLD: AAO3265
	Chile, Region Metropolitana, E of El Volcán	♀	CCDB-09858-H04	BOLD: AAO3265
	Chile, Region Metropolitana, E of El Volcán	♀	CCDB-22009-H11	BOLD: AAO3265
<i>C. lucens</i>	Chile, Region IV, 7km N of Los Vilos	♂	CCDB-28314-E04	BOLD: ADC8390
	Chile, Region VII, Laguna del Temo	♂	CCDB-28313-G01	BOLD: ADC8390
	Chile, Region VIII, E of Antuco	♀	CCDB-28314-E02	BOLD: ADC8390
<i>C. mastochila</i>	Argentina, Catamarca, 8km S of Chapillitas	♀	CCDB-15259-B02	BOLD: ABW4685
<i>C. musculus</i>	Argentina, Chubut, Trevelin	♀	CCDB-22014-B07	BOLD: ACW2084
	Argentina, Chubut, Trevelin	♂	CCDB-22009-F11	BOLD: ACW2084

	Argentina, Chubut, Trevelin	♂	CCDB-22014-B09	BOLD: ACW2084
	Chile, Region IX, Liucura	♀	CCDB-28315-C08	BOLD: ACW2084
<i>C. nigriritulus</i>	Argentina, Chubut, Trevelin	♀	ARG-14490-22	BOLD: AAV9330
	Chile, Region IV, E of Las Temeras	♂	CCDB-28316-D12	BOLD: AAV9330
	Chile, Region VII, Tregualemu	♀	CCDB-28315-D03	BOLD: AAV9330
	Chile, Region VII, Tregualemu	♂	CCDB-09984-A10	BOLD: AAV9330
	Chile, Region VII, Vado Estero los Molongos	♀	CCDB-28313-F07	BOLD: AAV9330
	Chile, Region VIII, W of Parque Nacional Laguna del Laja	♀	CCDB-28314-D12	BOLD: AAV9330
<i>C. nigropilosus n. sp.</i>	Chile, Region XV, 1.5km SE Campamento Planchones	♀	CCDB-28237-D04	BOLD: ACU7011
	Chile, Region XV, 1.5km SE Campamento Planchones	♂	CCDB-22014-F10	BOLD: ACU7011
	Chile, Region XV, Quebrada Cardones	♀	CCDB-22015-D09	BOLD: ACU7011
	Chile, Region I, NE of Huara	♀	CCDB-28237-G09	BOLD: ACU7011
<i>C. patagonicus</i>	Argentina, Chubut, Trevelin	♀	ARG-14490-19	BOLD: AAO3408
	Chile, Region IX, Questa las Raices	♂	CCDB-19991-B05	BOLD: AAO3408
<i>C. quehu</i>	Chile, Region II, Llullaillaco	♀	CCDB-28315-H07	BOLD: ACK8809
	Chile, Region II, Llullaillaco	♀	CCDB-28315-H09	BOLD: ACK8809
<i>C. rutilans</i>	Chile, Region II, 20km N of San Pedro de Atacama	♀	CCDB-09984-B03	BOLD: AAI9251
	Chile, Region II, 20km N of San Pedro de Atacama	♀	CCDB-09984-B04	BOLD: AAI9251
<i>C. simulatus n. sp.</i>	Chile, Region XV, Pucará Belén	♂	CCDB-22014-D02	BOLD: AAV8097
	Chile, Region I, 23km E of Pozo Almonte	♀	CCDB-22014-F12	BOLD: AAV8097
	Chile, Region I, Mamiña	♂	CCDB-22014-D06	BOLD: AAV8097
	Chile, Region I, Mamiña	♀	CCDB-28231-F06	BOLD: AAV8097
	Chile, Region I, Parca	♂	CCDB-22015-C11	BOLD: AAV8097
	Chile, Region I, Tambo	♂	CCDB-09981-D01	BOLD: AAV8097
<i>C. sulcatus</i>	Chile, Region IV, Los Vilos	♂	CCDB-09866-D03	BOLD: AAO3474
	Chile, Region IV, Los Vilos	♂	CCDB-28231-B12	BOLD: AAO3474
<i>C. sulcatus</i>	Chile, Region IV, Los Vilos	♂	CCDB-28237-E11	BOLD: AAO3474
	Chile, Region IV, Los Vilos	♂	CCDB-28239-E08	BOLD: AAO3474
<i>C. ventricarinatus n. sp.</i>	Chile, Region XV, 5km S of Putre	♂	CCDB-28237-H04	BOLD: ACK8653
	Chile, Region XV, Pucará Belén	♂	CCDB-22014-A07	BOLD: ACK8653
	Chile, Region XV, Putre	♂	CCDB-28237-A09	BOLD: ACK8653

**Table S2.** List of the *Colletes* species and the floral associations retrieved from the specimens' collection labels.

Species	Plant family	Plant species	Locality	Month
<i>Colletes atacamensis</i>	Leguminosae	<i>Caesalpinia</i> sp.	Chile – Region I: 23km E of Pozo Almonte	September
<i>C. atripes</i>	Loasaceae	<i>Nasa triphylla</i> (Juss.) Weigend	Chile – Region II: 16km N of Taltal	October
	Solanaceae	<i>Nolana</i> sp.	Chile – Region II: SE of Taltal	November
			Chile – Region III: Pq. N. Llanos de Challe	October
<i>C. cognatus</i>	Leguminosae	<i>Trifolium repens</i> L.	Argentina – Chubut: INTA Trevelin	December, January
<i>C. cyanescens</i>	Anacardiaceae	<i>Schinus patagonica</i> (Phil) I.M. Jhonst. ex Cabrera	Argentina – Chubut: INTA Trevelin	November
	Compositae	<i>Taraxacum campylodes</i> G.E. Haglund	Argentina – Chubut: INTA Trevelin	October, November
	Glossulariaceae	<i>Ribes magellanicum</i> Poir.	Argentina – Chubut: INTA Trevelin	November
	Leguminosae	<i>Cytisus scoparius</i> (L.) Link	Argentina – Chubut: INTA Trevelin	October, November
	Loasaceae	<i>Loasa tricolor</i> Ker Gawl.	Chile – Region IV: 7km S of Tiltal	October
			Chile – Region IV: N of Los Hornos	October
			Chile – Region IV: Parque Nacional Fray Jorge	October
			Chile – Region IV: Pichicuy	October
			Chile – Region IV: Ponte Samo Alto	October
			Chile – Region IV: Quebrada Seca	October
<i>C. cyaniventris</i>			Chile – Region V: Colliguay	October
	Proteaceae	<i>Lomatia hirsuta</i> (Lam.) Diels	Argentina – Chubut: INTA Trevelin	October, November
	Rhamnaceae	<i>Colletia spinosissima</i> J.F. Gmel	Chile – Region Metropolitana: Caleu	January
<i>C. flaminii</i>	Leguminosae	<i>Adesmia</i> sp.	Chile – Region VII: W of Laguna del Maule	January
<i>C. flavipilosus</i> n. sp.	Boraginaceae	<i>Phacelia</i> sp.	Chile – Region V: Portillo	December
			Chile – Region VII: Laguna del Teno	February
			Chile – Region Metropolitana: Valle Nevado	December
	Loasaceae	<i>Loasa filicifolia</i> Poepp.	Chile – Region VII: Laguna del Maule	January
	Malvaceae	<i>Tarasa operculata</i> (Crav.) Kaprov.	Chile – Region I: 12 SW of Chusmiza	September
<i>C. kuhlmanni</i> n. sp.	Boraginaceae	<i>Phacelia</i> sp.	Chile – Region Metropolitana: Farellones	

			Chile – Region Metropolitana: Valle Nevado	December
			Chile – Region VII: Laguna del Teno	February
	Compositae	<i>Baccharis</i> sp.	Chile – Region V: 60km E of Rio Blanco	December
		<i>Solidago</i> sp.	Chile – Region Metropolitana: Cuna Gallego Valley	January
		<i>Cistanthe salsoloides</i>		
	Portulacaceae	(Barnéoud Carolin ex M.A. Hershkovitz	Chile – Region II: Quebrada de Taltal	October
	Solanaceae	<i>Nolana</i> sp.	Chile – Region III: Potrerillos	October
<i>C. lucens</i>	Apiaceae	<i>Eryngium paniculatum</i> Cav. & Dombey ex F. Delaroche	Chile – Region IX: Maite Bajo	January
<i>C. mastochila</i>	Loasaceae	<i>Caiphora cirsiifolia</i> C. Presl	Chile – Region XV: Putre	February
<i>C. musculus</i>	Compositae	<i>Baccharis obovata</i> Hook. & Arn.	Argentina – Chubut: INTA Trevelin	December
	Glossulariaceae	<i>Ribes magellanicum</i>	Argentina – Chubut: INTA Trevelin	November
	Leguminosae	<i>Trifolium repens</i>	Argentina – Chubut: INTA Trevelin	December
<i>C. nigrifolius</i>	Escalloniaceae	<i>Escallonia virgata</i> (Ruiz & Pav.) Pers.	Argentina – Chubut: INTA Trevelin	January
<i>C. nigropilosus</i> n. sp.	Compositae	<i>Baccharis scandens</i> Less.	Chile – Region XV: Zapahuira	January
	Leguminosae	<i>Medicago sativa</i> L.	Chile – Region I: Codpaquilla	April
<i>C. patagonicus</i>	Leguminosae	<i>Trifolium repens</i>	Argentina – Chubut: INTA Trevelin	December
<i>C. rutilans</i>	Compositae	<i>Taraxacum</i> sp.	Ecuador – Loja: Loja	October
<i>C. simulatus</i> n. sp.	Leguminosae	<i>Caesalpinia</i> sp.	Chile – Region I: 23km E of Pozo Almonte	September
<i>C. sulcatus</i>	Loasaceae	<i>Loasa tricolor</i>	Chile – Region IV: Puente Samo Alto	October
			Chile – Region IV: Quebrada Seca	October

## Chapter 4: A revision of *Colletes* Latreille (Hymenoptera: Colletidae: Colletinae) from Brazil, Paraguay and Uruguay<sup>1</sup>

Rafael R. Ferrari

### Abstract

The species of *Colletes* Latreille from Brazil, Paraguay and/or Uruguay are revised through an integrative approach to taxonomy combining morphological and molecular data to delineate species. Herein, the following 19 species are recognized and illustrated, eight of them described as new: *C. altimontanus* Ferrari & Silveira, *C. argentinus* Friese, *C. chicoi* **n. sp.**, *C. cyaneus* Holmberg, *C. ferenudus* **n. sp.**, *C. flagellaris* **n. sp.**, *C. furfuraceus* Holmberg, *C. hawkingi* **n. sp.**, *C. imbricatus* **n. sp.**, *C. kerri* Moure, *C. meridionalis* Schrottky, *C. michenerianus* Moure, *C. ornatus* Schrottky, *C. pampeanus* **n. sp.**, *C. petropolitanus* Dalla Torre, *C. rufipes* Smith, *C. rugicollis* Friese, *C. sertanicola* **n. sp.**, and *C. sexangulus* **n. sp.** To facilitate their recognition, diagnoses, detailed descriptions and redescriptions, and a fully-illustrated key for all species are provided.

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## Introduction

This revision is the second part of a comprehensive study of which the main goal is to revise all the South American species of *Colletes* Latreille, 1802 (Colletidae: Colletinae). Currently, *Colletes* contains 510 valid species worldwide (Ascher & Pickering 2018), 80 of them known from South America (Moure *et al.* 2007; Moure *et al.* 2012), where the genus most likely originated (Kuhlmann *et al.* 2009; Almeida & Danforth 2011). In a recent publication, I revised the species of the genus found in Chile and described eight new ones for the country (Ferrari 2017). The present study is a taxonomic revision of the *Colletes* species distributed in Brazil, Paraguay and/or Uruguay. Together, these three countries cover an area of approximately 9,100,00 km<sup>2</sup>, corresponding to a little more than half of the entire South American territory.

Even though some taxonomic treatments encompassing the *Colletes* fauna of the eastern portion of South America have already been published (Schrottky 1902, 1907; Moure & Urban 2002; Ferrari & Silveira 2015), our overall understanding of the actual diversity of these interesting bees remains very poor. In an early checklist, Schrottky (1902) recorded six species (including one subspecies) from Brazil. Later, the same author (Schrottky 1907) listed five species from Paraguay: 1) *C. petropolitanus* Dalla Torre 1896 and *C. ornatus* Schrottky, 1902 that had originally been described from Brazil; 2) *C. patagonicus* Schrottky, 1907 and *C. bicolor* Smith, 1879 from Chile and Argentina the occurrence of which in Paraguay seems very unlikely; and 3) *C. semicyanea* Spinola, 1851 that was later transferred to *Leioproctus* (*Reedaspis*) Michener, 1989 (Colletidae: Neopasiphaeinae). In their catalog of the neotropical Colletini, Moure & Urban (2002) listed ten *Colletes* species as having geographical distribution in Brazil, Paraguay and/or Uruguay. More recently, Ferrari & Silveira (2015) described a new species (*C. altimontanus*) from southeastern Brazil, revalidated a previously described one (*C. argentinus* Friese, 1908), and synonymized *C. externsicornis* Vachal, 1909 under *C. meridionalis* Schrottky, 1902, thus bringing the number of *Colletes* species known to occur in these three countries to eleven.

In this revision, I redescribe and illustrate both sexes of all eleven species, and describe eight new ones for eastern South America. To facilitate their identification, a fully illustrated taxonomic key is given.

## Materials and Methods

### *Studied material*

To conduct the present revisionary study, I examined material from the following collections (curator and/or collection manager in parenthesis):

**AMNH** – American Museum of Natural History, New York, USA (J. Rozen and C. Smith).

**CNC** – The Canadian Natural Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada (S. Cardinal).

**DZUP** – Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (G. Melo).

**FMNH** – Field Museum of Natural History, Chicago, USA (C. Maier).

**INPA** – Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (M. Oliveira).

**LANUFSC** – Laboratório de Abelhas Nativas, Universidade Federal de Santa Catarina, Florianópolis, Brazil (J. Steiner).

**MACN** – Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (A. Roig-Alsina).

**MEUV** – Museu de Entomologia, Universidade Federal de Viçosa, Viçosa, Brazil (L. Campos).

**MNHP** – Muséum National d’Histoire Naturelle, Paris, France (C. Villemant and A. Touret-Alby).

**MZSP** – Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (C. Brandão).

**MZUEFS** – Museu de Zoologia, Universidade Federal de Feira de Santana, Feira de Santana, Brazil (C. Aguiar and S. Andena).

**NHMUK** – The Natural History Museum, London, England (D. Notton).

**PCYU** – Packer Collection, York University, Toronto, Canada (L. Packer).

**RPSP** – Coleção Entomologica Prof. J. M. F. Camargo, Universidade de São Paulo, Ribeirão Preto, Brazil (E. Almeida).

**SEMC** – Division of Entomology, University of Kansas, Lawrence, USA (M. Engel and J. Thomas).

**UFMG** – Coleções Taxonômicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (F. Silveira).

**ZMB** – Museum für Naturkunde, Berlin, Germany (M. Ohl and V. Richter).

As the focus this study is to revise the *Colletes* species from Brazil, Paraguay and Uruguay, the vast majority of the examined specimens are from these three countries. However, material from Argentina, Bolivia and Peru was also studied so that the actual geographical range of the species recognized herein could be more accurately understood and presented.

To facilitate recognition of primary type specimens in future studies, information from their labels are transcribed exactly as they are given, as follows: information on a single label is given between quotation marks; the end of each line in a label is indicated by a semicolon. Nevertheless, no text formatting (italics, bold, etc) was reproduced, even though capital letters were indicated whenever applicable. Data from the labels of other specimens (secondary type specimens included) are reproduced in the following order: **COUNTRY – country’s first-level administrative division**: municipality and/or specific locality, (geographic coordinates, when available), collection date as “dd/mm in Roman numbers/yyyy”, [collector(s)], number of specimens of each sex, {repository}. For each species, the geographical information of the examined material is listed alphabetically.

### *Integrative taxonomy*

This revision proceeded through an integrative approach to taxonomy, combining morphological data and DNA barcodes to delineate species, a practice that has become common amongst many melittologists lately (*e.g.* Gibbs 2011; Pauly *et al.* 2014; Rocha-Filho & Packer 2015; Monckton 2016; Ferrari 2017; Onuferko 2018). The external morphology of the bees was studied under a Olympus SZ61 stereomicroscope equipped with a Neewer Ring48 LED ring light. I also examined the male terminalia (*i.e.* hidden metasomal sterna and genital capsule) after clearing them overnight with 10% KOH solution within wells of a ceramic plate. Prior to dissection, males were relaxed in 15x15x5 cm plastic containers containing cotton balls soaked in water. Characters from the external morphology of both sexes and male terminalia (when available) were used to sort the specimens into operational taxonomic units (OTU's), which were then tentatively identified with the available keys (Schrottky 1902, 1907; Ferrari & Silveira 2015) and/or with comparison with the original descriptions of the South American species of *Colletes*.

Simultaneously, 658pb of cytochrome *c* oxidase subunit 1 (better known as the DNA barcode region) of selected representatives of each morphological OTU was sequenced (Table S1) to confirm distinction between interspecific from intraspecific variation, and facilitate sexual association. The right mid leg of the bees were sent in 96-well plates containing absolute ethanol to the Canadian Centre for DNA Barcoding (University of Guelph) for DNA extraction, amplification and sequencing. DNA barcodes were uploaded to the Barcode of Life Data System (BOLD) online database (Ratnasingham & Herbert 2007), and then clustered into molecular OTUs in two steps: firstly, sequences were automatically checked for quality (*i.e.* total length and number of ambiguous nucleotides) by BOLD, and if minimum quality was detected then they were assigned a Barcode Index Number (BIN) (Ratnasingham & Herbert 2013); secondly, I constructed a neighbor-joining tree using only the BIN-complaint barcodes. This analysis was carried out in BOLD's workbench, using the algorithm Muscle (Edgar 2004) to align the sequences and Kimura 2 Parameter (Kimura 1980) as nucleotide substitution model.

Whenever morphological and molecular data were inconsistent with one another the former was prioritized over the latter. If morphologically indistinguishable specimens of a single morphological OTU were assigned different BINs and/or were placed at separate clusters in the NJ tree, but additional scrutiny of their external morphology and male terminalia failed to provide further support for the molecular data, then a single species was recognized nonetheless. The same approach has been used before in various other revisionary works on bees (*e.g.* Gibbs 2009, 2010; Ferrari 2017; Onuferko 2018). No case of multiple morphological OTUs being grouped as a single molecular OTU (*i.e.* MERGE; see Ratnasingham & Herbert 2013) was observed.

The actual identity of each recognized OTU was ultimately determined by comparing them with the primary type specimens of the previously described *Colletes* species known to occur in eastern South America. All were examined, except those of *C. speculiventris* Cockerell, 1917a and *C. punctatissimus* Schrottky, 1902 which have been reported (Moure & Urban 2002; Moure *et al.* 2007) to be deposited at the National Museum of Natural History and MZSP, respectively, but could not be located there. Neither of the two species, however, are considered valid currently (refer to synonymies, below).

## *Terminology and species (re)descriptions*

Terminology used herein is consistent with that in my paper on the Chilean *Colletes* (Ferrari 2017), which ultimately followed Michener (2007) except: frons, vertex and gena are referred to as frontal, vertexal and genal areas, respectively (following Prentice 1998); and the basal area of propodeum and posterior surface of propodeum are referred to as horizontal and vertical surfaces of the metapostnotum, respectively. Terminology for surface sculpture follows Harris (1979), except that the term ‘striate’ is herein used to define a series of short, somewhat thick carina rather than impressed sculpture. Terminology for leg surfaces follows Aguiar & Gibson (2010).

The species descriptions and redescriptions given herein follow the same format as in Ferrari (2017). I provide a full, detailed description/redescription of the female of each species followed by a shorter description of the male where only the differences in relation to the former are listed. Puncture spacing is given in terms of the relative size of the puncture diameters ( $d$ ) and the interspaces ( $i$ ) among them, as follows: sparsely punctate ( $i > 2d$ ); moderately sparsely punctate ( $i = 1.5 - 2d$ ); moderately densely punctate ( $i = 1 - 1.5d$ ); densely punctate ( $i < d$ ); crowded (interspaces sharp). Pubescence length is compared to the diameter of the median ocellus (MOD), and given as follows: minute ( $< 0.5 \times \text{MOD}$ ); short ( $= 0.5 - 1 \times \text{MOD}$ ); moderately short ( $= 1 - 1.5 \times \text{MOD}$ ); moderately long ( $= 1.5 - 2 \times \text{MOD}$ ); long ( $= 2 - 2.5 \times \text{MOD}$ ); very long ( $> 2.5 \times \text{MOD}$ ). Body measurements were taken using a calibrated micrometer mounted on the stereomicroscope’s ocular lens; general dimensions (for example, body length) are given as absolute measurements in millimeters, whereas the diagnostic structures (for example, hind basitarsus width and length) are given as relative measurements expressed as ratios. Antennal flagellomeres and metasomal terga and sterna are abbreviated as F, T and S followed by appropriate numbers. Upper and lower interocular distances are abbreviated as UID and LID, respectively.

The International Commission on Zoological Nomenclature is herein referred to as “ICZN”, and the 4th edition of the International Code of Zoological Nomenclature is abbreviated as “the Code” (ICZN 1999).

### *Photographs and range maps*

The photographs provided in this study were taken using a Visionary Digital BK Plus Lab System with a Canon EOS 5D Mark II digital camera and Canon Macro MP-E 65mm lens. To image the male terminalia, Canon Extender EF 2x was connected to the camera to augment its magnification. Photographs from various planes of focus were taken with a P-51 Cam-Lift high precision Linear Actuator using the software P51 Camlift Controller v.2.6. Individual slices were imported with Adobe Lighroom v4.4 and finally exported to Helicon Focus v.5.3.3 where they were amalgamated into a single, multi-focus image. Final images were edited, and mounted into plates, in Adobe Photoshop v13.0.1.

Range maps were produced in QGIS v.2.18.5. Only the records obtained directly from the specimens' labels were plotted onto the maps, although those reported in the literature are also given in the "Range" sections. The biogeographical distributions of species are presented according to the regionalisation of the Neotropical region proposed by Morrone (2014).

### *Floral data*

The floral data were obtained from either the literature (*e.g.* Jöergensen 1912a, b; Schlindwein 1995, 1998) or the specimens' labels. The list of the floral hosts reported herein for the first time, as well as the collection data of the specimens from which the new associations were established, is given in Table S2. To ensure that the botanic classification is up-to-date, I consulted the Plant List's website (The Plant List 2018).

## **Taxonomy**

### ***Colletes* Latreille, 1802**

Note: Synonymic list modified from Michener (2007):

*Colletes* Latreille, 1802.

Type species: *Apis succincta* Linnaeus, 1758.



*Evodia* Panzer, 1806.

Type species: *Apis calendarum* Panzer, 1806 (junior synonym of *Apis succincta* Linnaeus, 1758).

*Monia* Westwood, 1875 (junior homonym of *Monia* Gray, 1850).

Type species: *Monia grisea* Westwood, 1875.

*Monidia* Cockerell, 1905 (new name for *Monia* Westwood (not Gray)).

*Colletes* (*Ptilopoda*) Friese, 1921.

Type species: *Colletes maculipennis* Friese, 1921 (junior synonym of *Colletes spiloptera* Cockerell, 1917b).

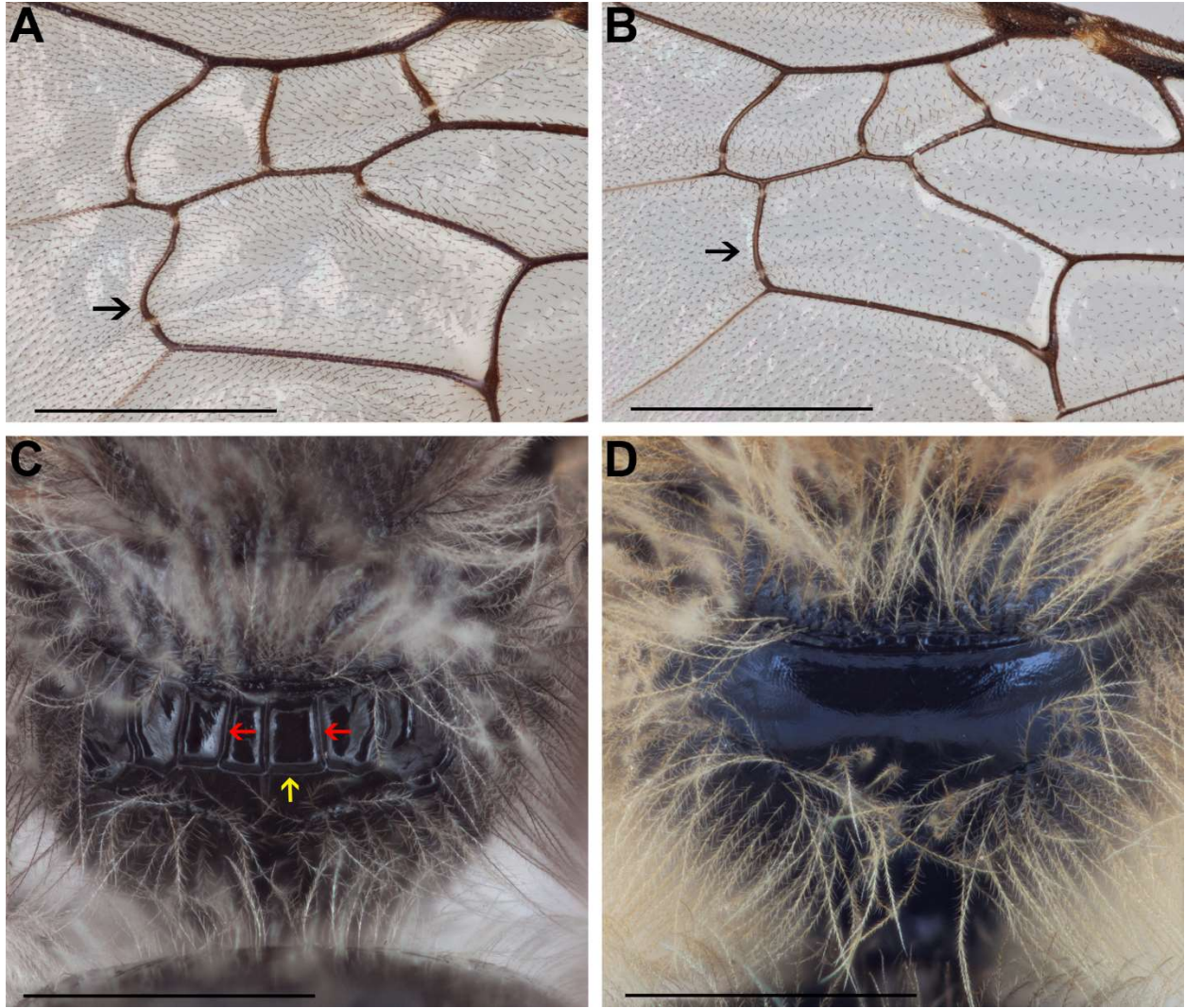
*Colletes* (*Puncticolletes*) Noskiewicz, 1936.

Type species not designated thus not valid.

*Rhynchocolletes* Moure, 1943.

Type species: *Rhynchocolletes albicinctus* Moure, 1943.

**Diagnosis:** Both sexes of the genus can be fairly easily diagnosed due to the characteristic sigmoidal shape of the vein 2m-cu (also referred to as the second recurrent vein) of the forewing with the posterior part arcuate outwardly, and anterior part slightly curved inwardly (Fig. 1A). In some species of *Rhynchocolletes* Moure, 1943 (sensu Moure *et al.*, 2007, 2012) – the only other genus of Colletinae with representatives in eastern South America – the posterior part of the 2m-cu vein may be slightly arcuate, however, its anterior part is always straight and thus the vein is never sigmoidal (Fig. 1B). *Hemicotelles* Toro & Cabezas, 1977 and *Xanthocotelles* Toro & Cabezas, 1978 are both endemic to Chile and western Argentina (Michener 2007; Moure *et al.* 2007; Ascher & Pickering 2018) and therefore cannot be confused with the *Colletes* species found in eastern South America. In *Colletes*, the horizontal surface of the metapostnotum is divided into a series of pits by longitudinal carinae, and is separated from the vertical surface by a transverse carina that may be complete or interrupted medially (Fig. 1C). In *Rhynchocolletes*, the longitudinal carinae and transverse carina are absent, and the horizontal and vertical surfaces of metapostnotum are separated from each other only by a change in slope (Fig. 1D).



**Figure 1.** Lateral view of forewing (A–B) and posterior view of metapostnotum (C–D). (A) Vein 2m-cu (black arrow) sigmoid in *Colletes*; (B) vein 2m-cu (black arrow) only slightly arcuate outwards in *Rhynchocolletes*. (C) Horizontal surface divided into pits by a series of longitudinal carinae (red arrows) and separated from vertical surface by transverse carina (yellow arrow) in *Colletes*; (D) horizontal surface without longitudinal carinae and separated from vertical surface by a change in slope in *Rhynchocolletes*. Scale bars = 1mm.

## Species list

### *Colletes altimontanus* Ferrari & Silveira, 2015

(Figs. 2, 3, 4, 48A, 54A)

*Colletes altimontanus* Ferrari & Silveira, 2015: 249; Ascher & Pickering 2018.

Holotype ♀ examined. (UFMG).

**Diagnosis:** *Colletes altimontanus* can be diagnosed through the combination of mesosoma with off-white and black hairs intermixed and T2–T5 discs covered with off-white appressed hairs.

*Colletes altimontanus* is most similar to *C. petropolitanus* in that the mesosoma of both species is covered with off-white and black hairs intermixed, the tegula is dark-brown and the forewing has a hyaline membrane and dark-brown venation. These species, however, can be distinguished from each other by labral mid concavity margined laterally by longitudinal ridges in *C.*

*altimontanus* (labral concavity not margined laterally by ridges in *C. petropolitanus*); clypeal mid-longitudinal area depressed in *C. altimontanus* (clypeus without mid-longitudinal depression in *C. petropolitanus*); and T2–T5 discs with appressed plumose hairs in *C. altimontanus* (T2–T5 discs without such hairs in *C. petropolitanus*).

**Redescription:** FEMALE (Figs. 2A, 2C, 2E):

*Dimensions (mm):* Approximate body length 8.8–9.7; head width 3.3–3.5; head length 2.5–2.6; intertegular distance 2.4–2.6; forewing length 7.2–7.6.

*Colouration:* Black except distal 1/3 of mandible reddish-brown. Tegula, wing venation (except veins C and R of forewing black), stigma, femora, tibiae, tarsi (except dorsal surface of distitarsi and tarsal claws pale-brown) and ventrally reflexed lateral areas of T1 dark-brown. Marginal zones of metasomal terga (except that of T6 black) and sterna pale-brown. Tibial spurs pale-yellow.

*Structure:* Labrum medially concave; concavity margined laterally by longitudinal ridges. Clypeal mid-longitudinal area deeply and very narrowly (0.3x MOD) depressed on upper half; depression progressively shallower and broader (maximum width 1.5x MOD) towards lower margin. Malar area ~0.8x as long as basal depth of mandible (47:59).



**Figure 2.** *Colletes altimontanus* Ferrari & Silveira, 2015. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.



Hypostomal carina short and flat. F1  $\sim 1.3\times$  as long as its apical width (32:24). UID:LID (64:59). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum modified as a long spine. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum  $\sim 0.6\times$  as long as metanotum (28:44); metapostnotal pits well-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 4\times$  longer than broad (55:14). Outer rami of hind tarsal claws  $\sim 2\times$  as long as inner rami (15:8). Marginal zone of T1 flat. Marginal zone of S6 not depressed.

*Pubescence:* Head with plumose, erect, long, off-white and black hairs intermixed (except mandible with fuscous, moderately long setae); those hairs suberect on lateral slopes of clypeus, almost entirely black on frontal area; vertexal area with very long black hairs; genal area with mostly off-white, moderately long hairs (except long towards proboscidal fossa). Mesosoma with plumose, erect, very long, off-white and black hairs intermixed; those hairs moderately short on pronotal lobes and long on mesoscutum and scutellum; lateral surface of propodeum with off-white, appressed, short hairs. Legs with pale-yellow hairs; trochanters and femora with plumose, erect, moderately long hairs (except hind trochanter with very long hairs); femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; tibiae with suberect, short setae (except posterior surface of front tibia and dorsal surface of hind tibia with erect, moderately long setae); basitarsi with erect, moderately short setae (except posterior margins of mid and hind basitarsi with long setae). Metasomal terga covered with off-white, plumose, appressed, short hairs; T1 entirely and T2–T3 laterally also with plumose, erect, long hairs (except T2–T3 with moderately short hairs); T4–T5 also with black, long, setae laterally; T6 with black, suberect, short setae. Metasomal sterna with pale-yellow hairs; S1 with plumose, erect, moderately long hairs; S2–S6 discs with erect, moderately short setae; S2–S5 marginal zones with a transverse line of plumose, suberect hairs.

*Surface sculpture:* Clypeal mid-longitudinal depression sparsely and finely punctate; adjacent convex area longitudinally coarsely striate. Supraclypeal area imbricate. Malar area longitudinally striate. Paraocular area punctures crowded and moderately coarse below; dense and moderately fine above; interspaces smooth throughout. Frontal area densely and moderately coarsely punctate; interspaces rugulose. Vertexal area punctures crowded and moderately fine

near lateral ocellus; sparse and minute towards eye; interspaces smooth. Mesoscutum densely and coarsely punctate (except sparsely punctate posteromedially). Scutellum punctures crowded and coarse (except moderately dense medially); interspaces smooth. Metanotum densely and moderately coarsely punctate; interspaces smooth. Mesepisternum densely and coarsely punctate near scrobe; sparsely and moderately finely punctate towards ventral surface; interspaces smooth (except rugulose anterior to episternal groove). Metepisternum with oblique carinae mid-anteriorly; rugose above; densely and moderately finely punctate below (interspaces smooth). Lateral surface of propodeum densely and finely punctate anteriorly (interspaces rugulose); rugose posteriorly. Vertical surface of metapostnotum transversely striate above. Metasomal terga moderately sparsely and minutely punctate (except T1 sparsely punctate). S2–S5 moderately densely and finely punctate (except largely impunctate anteriorly and mid-longitudinally); interspaces imbricate throughout. S6 densely and moderately coarsely punctate at midlength; interspaces imbricate.

MALE (Figs. 2B, 2D, 2F). As in female, except for usual secondary sexual characteristics and as follows:

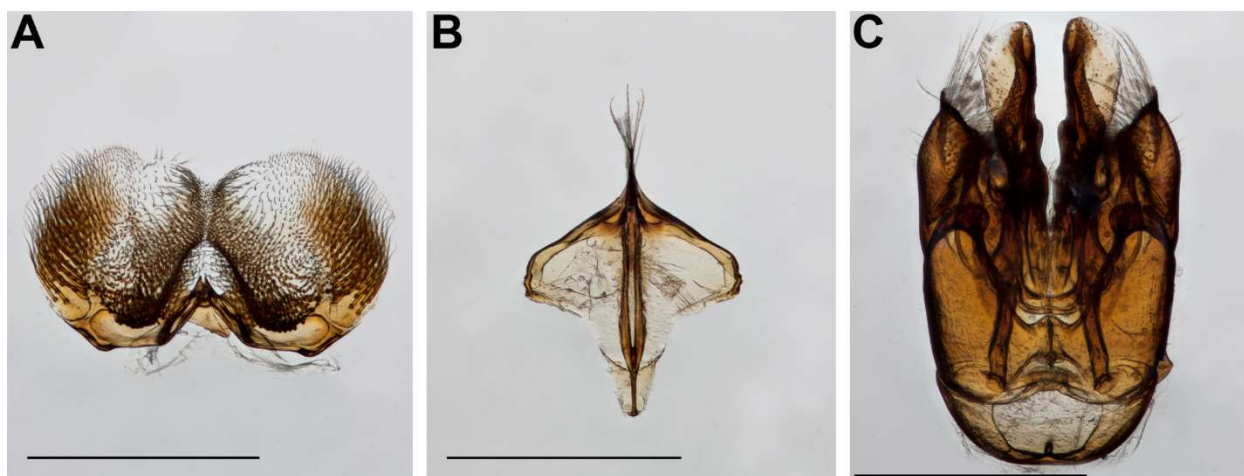
*Dimensions (mm)*: Approximate body length 7.9–8.3; head width 2.8–3.0; head length 2.2–2.3; intertegular distance 1.8–2.0; forewing length 6.4–6.7.

*Colouration*: Ventral surface of F2–F8 dark-orange. Front tarsus, mid and hind femora, tibiae and tarsi pale-brown. Proximal half of tarsal claws and marginal zones of T1–T6 pale-yellow. Wing venation (except vein R of forewing black) and stigma pale-brown.

*Structure*: Clypeal mid-longitudinal depression moderately broad below (= MOD). Malar area ~1.4x as long as basal depth of mandible (46:33). F1 ~1.1x as long as its apical width (36:33). UID:LID (60:46). Horizontal surface of metapostnotum ~0.5x as long as metanotum (22:42). Hind basitarsus ~4x longer than broad (49:11). Outer rami of hind tarsal claws ~4.5x as long as inner rami (15:8). S7, S8 and genital capsule as in Figs. 3A, 3B, 3C, respectively.

*Pubescence*: Lateral surface of propodeum with erect, long hairs. Plumose, appressed hairs on T1 restricted to marginal zone. S6 with plumose hairs.





**Figure 3.** Dorsal view of the male terminalia of *Colletes altimontanus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Surface sculpture:* Clypeal mid-longitudinal depression densely punctate; adjacent convex area smooth. Vertexal area densely punctate near eye. Metanotum moderately densely punctate. Vertical surface of metapostnotum smooth above. T1 moderately densely and moderately finely punctate. T2 finely punctate. S6 densely and finely punctate laterally; mid-longitudinal area largely impunctate.

**Material studied:** *Primary type specimen:* Holotype ♀ – “Abelhas Espinhaço; Pq. E. do Rio Preto; 10146-29742”. “São Gonçalo do Rio Preto MG; BRASIL 19/10/2004; A.A.Azevedo”. “HOLOTYPUS; *Colletes altimontanus*; Ferrari & Silveira, sp. nov.”. {UFMG}.

*Secondary type specimens:* Paratypes ♀♀ and ♂♂: **BRAZIL – Bahia:** Abaeté, 14/x/1996, [E. Neves], 1♀ {UFMG}; idem, except 15/xi/1996, 1♀; idem, except 30/xi/1996, 1♂. **Minas Gerais:** Belo Horizonte, Parque das Mangabeiras, 23/i/1997, [F. Silveira], 1♂, {UFMG}. Belo Vale, 26/vii/1986, [G. Melo], 1♀1♂, {MEUV}. Brumadinho, Parque Estadual da Serra do Rola-Moça, 9/xi/2004, [A. Azevedo], 1♀1♂, {UFMG}; idem, except 10/xi/2004, 1♀1♂; Serra da Moeda, 12/xii/1997, [F. Silveira], 1♀, {UFMG}; idem, except [Oliveira & Almeida], 1♀; idem, except [R. Oliveira], 1♀; idem, except 21/iii/1998, 1♀; idem, except 29/iii/1998, 1♀; idem, except 23/v/1998, 1♀; idem, except 25/vii/1998, 1♂; idem, except 10/i/1999, 1♀; idem, except 27/xii/1997, [E. Almeida], 1♂; idem, except 26/iv/1998, [Almeida & Guimarães], 2♀♀;

idem, except 18/xii/1999, [E. Morato], 1♀. Catas Altas, Serra do Caraça, xi/1961, [Kloss, Lenko, Martins & Silva], 1♂, {MZSP}. Itacambira, 11/iii/2005, [R. Martins], 1♀, {UFMG}. Itamarandiba, Serra do Ambrósio, 29/vii/1997, [F. Silveira], 1♂, {UFMG}. Lima Duarte, Parque Estadual do Ibitipoca, 29/ix/2006, [A. Azevedo], 4♂♂, {UFMG}; idem, except 18/iii/2007, 1♀; idem, except 19/iii/2007, [M. Goulart], 2♀♀2♂♂. Nova Lima, COPASA/Mutuca, 7/viii/1999, [M. Pompeu], 1♂, {UFMG}; Parque Estadual da Serra do Rola-Moça, 16/xi/2004, [N. Fonseca], 1♂, {UFMG}. Poços de Caldas, xi/1961, [C. Elias], 3♀♀, {DZUP}. São Gonçalo do Rio Preto, Parque Estadual do Rio Preto, 23/ix/2003, [A. Azevedo], 1♀, {UFMG}; idem, except 19/x/2004, 2♀♀; idem, except 20/x/2004, 2♀♀1♂; idem, except 8/v/2006, 1♂; idem, except 10/v/2006, 1♀1♂. **Pernambuco:** Parque Nacional do Catimbau, 6/vi/2008, [M. Silva], 1♀, {UFMG}; idem, except 9/ix/2008, 1♂.

*Additional specimen:* **BRAZIL – Bahia:** Vitória da Conquista, Serra do Periperi, (-14.8333, -40.8166), 9/vi/2000, [Melo & Costa], 1♂, {MZUEFS}.

**Range:** BRAZIL (Bahia, Minas Gerais, Pernambuco). See also Fig. 4.

**Biogeographical distribution:** Chacoan dominion (Caatinga and Cerrado provinces), and Parana dominion (Parana Forest province) at altitudes of 700–1500m a.s.l.

**DNA barcode:** Unavailable.

**Floral hosts:** Lamiaceae – *Eriope crassipes* Benth. (this study), *Hypenia salzmännii* (Benth.) Harley (this study).

**Comments:** Uncommon species intimately associated with the Espinhaço mountain range in southeastern Brazil.



**Figure 4.** Geographical distribution of *Colletes altimontanus* (blue circles), *C. kerri* (red stars), and *C. pampeanus* sp. n. (green diamond). Scale bar approximately 250km.

***Colletes argentinus* Friese, 1908**

(Figs. 5, 6, 7, 46A, 46C, 47A, 47C, 53A)

*Colletes argentinus* Friese, 1908: 10; Jensen-Haarup 1908: 100; Strand 1909: 228, 1910: 457; Ducke 1912: 78; Schrottky 1913: 236; Cockerell 1917a: 438; Jörgensen 1909: 5, 1912a: 301, 1912b: 99; Rasmussen & Ascher 2008: 25; Torretta & Poggio 2013: 160; Ferrari & Silveira 2015: 257; Ascher & Pickering 2018; Lando *et al.* 2018: 4.

Lectotype ♂ examined. Designated by Moure & Urban (2002: 19). (ZMB).

*Colletes rugicollis* (*partim*); Moure & Urban 2002: 19; Moure *et al.* 2007: 687; Moure *et al.* 2012.

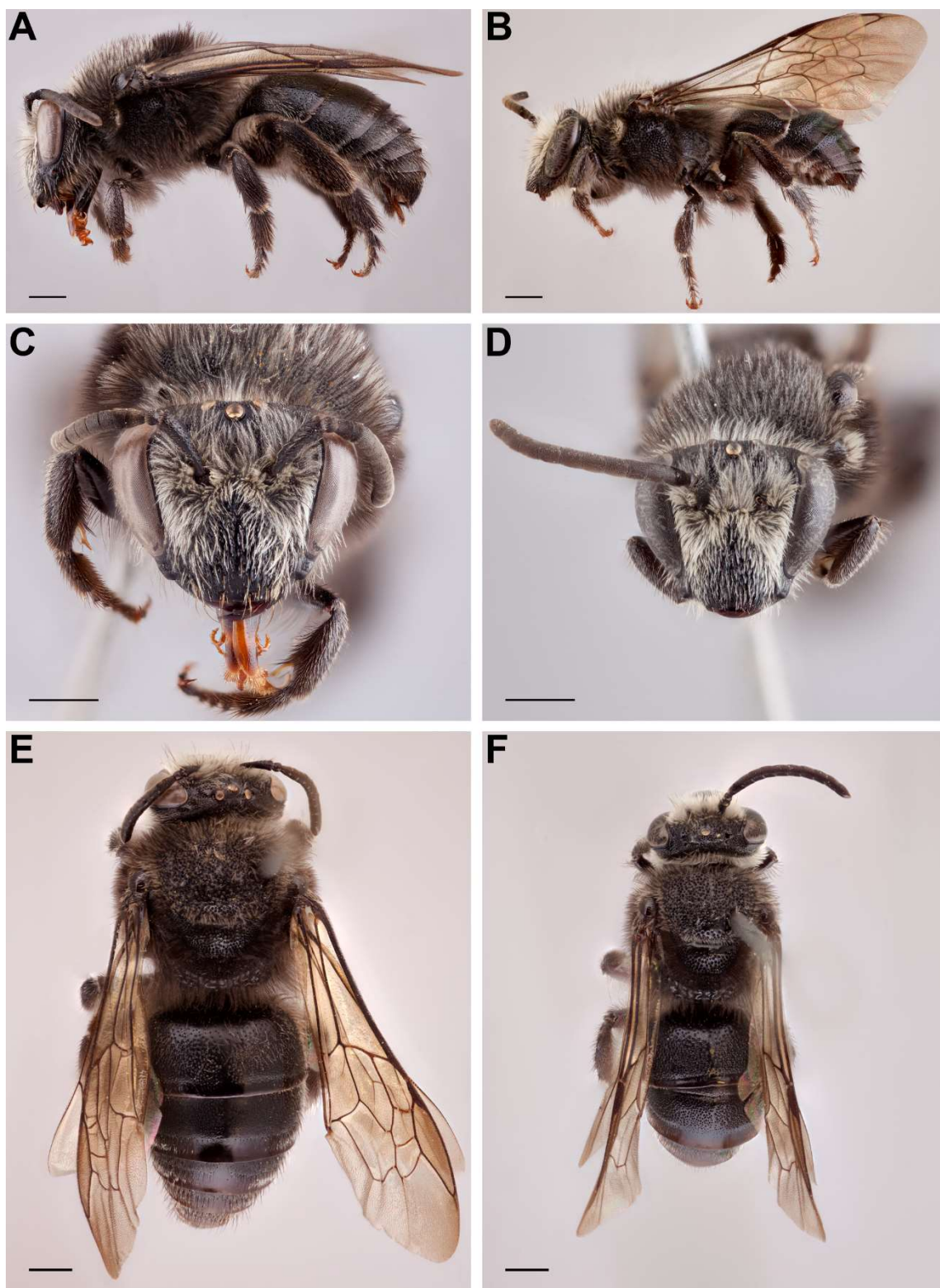
**Diagnosis:** *Colletes argentinus* can be diagnosed through the combination of hypostomal carina short and flat, and T1 marginal zone convex. *Colletes argentinus* is most similar to *C. rugicollis* in that both have a protrusion below the lateral ocellus, and T1 coarsely and densely punctate. However, *C. argentinus* can be readily differentiated from *C. rugicollis* by its hypostomal carina short and flat (hypostomal carina produced as a tall, concave lamella in *C. rugicollis*); and paraocular area with mostly off-white hairs (paraocular area with mostly pale-yellow hairs in *C. rugicollis*). The males of the two species can also be distinguished from each other by supraclypeal area sparsely punctate in *C. argentinus* (supraclypeal area densely punctate in *C. rugicollis*).

**Redescription:** FEMALE (Figs. 5A, 5C, 5E):

*Dimensions (mm):* Approximate body length 10.4–11.2; head width 3.1–3.3; head length 2.5–2.7; intertegular distance 2.8–3.1; forewing length 8.3–8.8.

*Colouration:* Black except distal half of mandible and tarsal claws reddish-brown. Tegula posterolaterally, tarsi (except basitarsi), hind tibial spurs, marginal zones of T1–T5, S6 mid-longitudinally and posteriorly dark-brown. Wing venation (except vein R of forewing black), mid tibial spurs pale-brown. Proximal half of tarsal claws, marginal zones of metasomal sterna pale-yellow.





**Figure 5.** *Colletes argentinus* Friese, 1908. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.

*Structure:* Labrum medially concave; concavity not margined laterally by longitudinal ridges. Clypeus without mid-longitudinal depression. Malar area  $\sim 0.45\times$  as long as basal depth of mandible (20:44). Hypostomal carina short and flat. F1  $\sim 1.1\times$  as long as its apical width (32:28). UID:LID (66:59). Frontal area with a protrusion below lateral ocellus. Vertexal area flat behind upper summit of compound eyes in lateral view. Dorsolateral angle of pronotum pointed. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum  $\sim 0.5\times$  as long as metanotum (29:56); metapostnotal pits well-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 2.6\times$  longer than broad (50:19). Outer rami of hind tarsal claws  $\sim 1.75\times$  as long as inner rami (14:8). Marginal zone of T1 convex. Marginal zone of S6 depressed.

*Pubescence:* Head with off-white, plumose, erect, moderately short hairs (except mandible with pale-yellow, suberect setae); paraocular, interantennal, frontal and vertexal areas with off-white and black hairs intermixed; genal area with fuscous, long hairs towards proboscidal fossa. Mesosoma with black, plumose, erect, moderately long hairs; those hairs long on mesepisternum, very long on upper margin of lateral surface of propodeum; pronotal lobe and mesoscutum with black and off-white hairs intermixed. Legs with black hairs; trochanters and femora with plumose, erect, long hairs (except moderately long on mid trochanter); femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; tibiae with short, suberect setae (except hind tibia with erect, moderately short setae); basitarsi with erect, moderately short setae (except posterior margins with long setae). Metasoma covered with black hairs (except T1 with off-white and fuscous plumose hairs intermixed); T2–T5 with suberect, minute setae on discs (except short on T4–T5), those setae erect, moderately short laterally; T6 with suberect, short setae throughout; S1 with plumose, erect, moderately long hairs; S2 with moderately long setae and short plumose hairs intermixed; S3–S6 with suberect, short setae on discs, S3–S5 with a line of plumose, short hairs near marginal zones.

*Surface sculpture:* Clypeus densely and coarsely punctate (interspaces smooth), except mid-longitudinal area largely impunctate (integument rugulose). Supraclypeal area moderately coarsely punctate; densely punctate below, largely impunctate above; interspaces imbricate. Malar area substrigulate. Paraocular area densely and moderately finely punctate (except moderately coarsely punctate towards antennal socket); interspaces rugulose throughout. Frontal



area punctures crowded and coarse; interspaces smooth. Vertexal area punctures crowded and moderately fine near lateral ocellus (interspaces rugulose); moderately fine punctures intermingled with minute ones towards eye (interspaces smooth). Mesoscutum, scutellum and mesepisternum punctures crowded and coarse (except mesoscutum only densely punctate posteromedially and scutellum sparsely and moderately finely punctate anteriorly); interspaces smooth throughout. Metanotum rugose. Metepisternum with oblique carinae mid-anteriorly; rugose elsewhere. Lateral surface of propodeum with punctures crowded and moderately coarse; interspaces rugulose. Vertical surface of metapostnotum rugose above. T1 densely and coarsely punctate (except finely punctate towards marginal zone and mid-longitudinal area largely impunctate); interspaces smooth. T2–T4 moderately densely and finely punctate; interspaces smooth. T5 densely and finely punctate. S2–S5 finely punctate; S2–S3 densely punctate, S4–S5 punctures crowded; interspaces smooth throughout. S6 densely and moderately finely punctate; interspaces smooth (except imbricate anteriorly and laterally).

MALE (Figs. 5B, 5D, 5F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 7.3–8.1; head width 2.5–2.8; head length 2.2–2.4; intertegular distance 2.0–2.3; forewing length 6.9–7.3.

*Colouration*: Legs dark-brown (except femora and trochanters black and outer surface of tarsi pale-brown). Ventrally reflexed lateral areas of T1–T2 mostly dark-brown. S2–S3 mid-longitudinally and posteriorly pale-brown. S6 evenly dark-brown.

*Structure*: Labral median concavity margined laterally by longitudinal ridges. Malar area ~0.65x as long as basal depth of mandible (26:40). F1 ~0.85x as long as its apical width (30:36). UID:LID (53:42). Vertexal area concave behind upper summit of compound eyes in lateral view. Horizontal surface of metapostnotum 0.85x as long as metanotum (34:40); metapostnotal pits poorly-delimited. Hind basitarsus ~2.7x longer than broad (43:16). Outer rami of hind tarsal claws 1.2x as long as inner rami (12:10). S7, S8 and genital capsule as in Figs. 6A, 6B, 6C, respectively.

*Pubescence*: Genal area with off-white hairs. Mesoscutal hairs as long as those of scutellum. Discs of T2–T5 with off-white to fuscous setae; those of S3–S5 erect and moderately short. Marginal zones of S2–S5 with off-white plumose hairs.



**Figure 6.** Dorsal view of the male terminalia of *Colletes argentinus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Surface sculpture:* Supraclypeal area sparsely punctate throughout; interspaces smooth. Paraocular area evenly moderately finely punctate. Vertexal area densely and moderately coarsely punctate throughout. T1 punctures crowded mid-longitudinally. T2 moderately coarsely punctate. T3 moderately finely punctate. . S2–S3 moderately densely punctate; S2 with imbricate interspaces anteriorly and laterally. S4–S5 densely punctate. S6 finely punctate.

**Material studied:** *Primary type specimen:* Lectotype ♂ – “Argentina; Mendoza; 10.2 1907; Jensen”. “*Colletes; argentinus*; 1907 Friese det.”. “Type” “Zool. Mus.; Berlin”. “LECTOTYPUS; *Colletes argentinus* ♂; Friese, 1908; Ferrari & Silveira, 2012”. <http://coll.mfn-berlin.de/u/;58f9b2>. {ZMB}.

*Secondary type specimens:* Paralectotypes ♂♂ – **ARGENTINA – Mendoza:** 4♂♂, {MNHP}.

*Additional specimens:* **ARGENTINA – Buenos Aires:** Burzaco, 27/iii/1974, [C. Vardy], 1♀1♂, {NHMUK}. **Catamarca:** 20km N of Andalgalá, (-27.4912, -66.3834), 14/ii/2003, [L. Packer], 1♀, {PCYU}. **Corrientes:** Parque Nacional Mburucuya, (-28.0314, -58.0614), 15/iii/2010, [N. Veiga], 1♂, {PCYU}. **Entre Ríos:** Liebig, [Zelich], 1♂, {AMNH}. **La Rioja:**

La Rioja, 20/viii/1916, [E. Giacomelli], 1♀1♂, {MACN}. **Salta:** Coronel Moldes, xii/1994, [Fritz], 1♀, {AMNH}. El Maray, i/1995, [Fritz], 2♂♂, {AMNH}. La Viña, iii/1992, [Fritz], 1♂, {AMNH}. Rosario de Lerma, x/1992, [Fritz], 3♂♂, {AMNH}; idem, except xi/1992, 3♂♂; idem, except xi/1993, 1♂. Sumalao, i/1993, [Fritz], 1♂, {AMNH}; idem, except xii/1994, 1♂; idem, except i/1996, 1♀. **Tucumán:** Tafi del Valle, 6/i/1970, [Vardy & Arguindeguy], 2♀♀2♂♂, {NHMUK}. **BRAZIL – Espírito Santo:** Santa Leopoldina, 4/iii/1964, [C. Elias], 1♀, {DZUP}. **Minas Gerais:** Baependi, Parque Estadual da Serra do Papagaio, 8/iv/2008, [F. Silveira], 1♀, {UFMG}; idem, except 9/iv/2008, 2♀♀; idem, except 10/iv/2008, 1♀. Belo Horizonte, COPASA/Barreiro, 24/ix/1999, [G. Sousa], 1♀, {UFMG}; Parque das Mangabeiras, 5/xii/1996, [J. Damasceno], 1♀, {UFMG}; idem, except 9/v/1997, 1♀. Cássia, Rancho do Popi, 28/iii/1999, [E. Almeida], 6♂♂, {UFMG}. Itajubá, 2/xii/1955, [M. Arié], 1♂, {DZUP}. Juiz de Fora, 11/iii/1985, [M. Garcia], 1♀, {MEUV}. Ouro Preto, 25/i/1985, [Melo, Soares & Morato], 1♂, {MEUV}. Passos, ii/1961, [C. Elias], 1♀1♂, {DZUP}; idem, except iii/1961, 11♀♀3♂♂; idem, except iv/1961, 2♂♂; idem, except 20/xi/1961, 1♀1♂; idem, except 24/ii/1962, 10♀♀1♂; 1/iii/1962, 5♀♀; idem, except 9/iii/1962, 1♀; idem, except 21/iii/1962, 1♀; idem, except iv/1962, 1♀; idem, except 21/v/1962, 1♂; idem, except 1/vi/1962, 1♀; idem, except 1/xi/1962, 1♂; idem, except 12/xi/1962, 5♂♂; idem, except 24/xii/1962, 1♀2♂♂; idem, except 5/i/1963, 1♀2♂♂; idem, except 16/i/1963, 1♀1♂; idem, except vi/1963, 2♀♀1♂; idem, except 24/x/1963, 1♀; idem, except 4/ix/1963, 2♀♀1♂; idem, except 16/xii/1963, 1♂; idem, except iii/1964, 2♂♂. Patrocínio, 5/x/1965, [C. Elias], 1♂, {DZUP}. Poços de Caldas, 23/xi/1962, [C. Elias], 1♀5♂♂, {DZUP}. Viçosa, Universidade Federal de Viçosa, 18/xi/1986, [G. Bastos], 1♀, {MEUV}; idem, except 8/iv/1988, 1♂; idem, except 25/xi/1988, 1♂; idem, except 14/xii/1988, 1♀; idem, except 11/ii/1989, 2♀♀; idem, except 25/ii/1985, 2♀♀4♂♂; idem, except 4/iii/1989, 1♂; idem, except 11/iii/1989, 1♀; idem, except 18/iii/1989, 1♀; idem, except 3/xii/1989, 1♂; idem, except 24/x/1987, [J. Cure], 1♂; idem, except 11/ii/1989, [J. Cure], 1♀; idem, except 18/x/1989, [A. Soares], 1♀2♂♂; idem, except 18/iii/1989, [F. Silveira], 2♂♂, {UFMG}; unspecified locality, 29/iv/1985, [G. Melo], 1♀, {MEUV}. **Paraná:** São Mateus do Sul, UN-SIX/Petrobrás, 23/i/2011, [R. Kamke], 1♀, {LANUFSC}. **Rio Grande do Sul:** 29km E of Santana do Livramento, (-30.8039, -55.2609), 14/xi/2016, [Ferrari & Freitas], 3♀♀, {PCYU}. Pelotas, 14/v/1958, [C. Biezanko], 1♂, {NHMUK}; idem, except 1/iii/1963, 1♀, {NHMUK}. **Santa Catarina:** Florianópolis, 12/xi/2007, [R. Kamke], 1♀, {LANUFSC}. Nova Teutônia,

2/xii/1937, [Plaumann], 1♂, {NHMUK}. **São Paulo:** Campinas, 30/xii/1991, [S. Pedro], 1♀, {RPSP}. **PARAGUAY – Alto Paraná:** Puerto Bertoni, 2/iv/1909, [A. Bertoni], 1♀, {NHMUK}; idem, except xii/1909, 1♀. **Guairá:** Reserva de Recursos Manejados Ybytyruzó, (-25.9514, -56.2206), 24/i/2007, [E. Willis], 1♂, {PCYU}. **Paraguarí:** Paraguarí, 4km SE of La Colmena, (-25.8471, -56.8127), 21/i/2007, [E. Willis], 1♂, {PCYU}. **URUGUAY – Tucuaembó:** 40km NW of Tucuaembó, 2/ii/1963, [J. Bouseman], 2♂♂, {AMNH}; idem, except 10/ii/1963, 1♀.

**Range:** ARGENTINA (Buenos Aires, Catamarca, Corrientes, Entre Ríos, La Rioja, Mendoza, Salta), BRAZIL (Espírito Santo, Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina, São Paulo), PARAGUAY (Alto Paraná, Guairá, Misiones, Paraguarí), URUGUAY (Tucuaembó). See also Fig. 7.

**Biogeographical distribution:** Chacoan dominion (Cerrado, Chacoan and Pampean provinces), Parana dominion (Parana Forest and *Araucaria* Forest provinces), and South American transition zone (Monte, Puna and Prepuna provinces) at altitudes of 0–2100m a.s.l.

**DNA barcode:** Available. BOLD: AAI9260 (3♀♀ and 3♂♂). Distance from the nearest neighbour (*C. rugicollis*): 2.89–4.03%.

**Floral hosts:** Compositae – *Baccharis salicina* Torr. & A. Gray (Jöergensen 1912a, 1912b (as *B. salicifolia* (Ruiz & Pav.) Pers.)), *B. pingraea* DC. (Jöergensen 1912b (as *B. serrulata* (Lam.) Pers.)). Leguminosae – *Hoffmanneseggia glauca* (Jöergensen 1912b (as *H. falcaria* Cav.)). Solanaceae – *Physalis* sp. (Friesse 1921), *Solanum didymum* Dunal. (Lando *et al.* 2018).

**Comments:** Relatively common species widely distributed in southeastern South America.

*Colletes argentinus* was synonymized with *C. rugicollis* by Moure & Urban (2002), a decision that was later sustained by other taxonomic treatments of the genus (Moure *et al.* 2007, 2012). However, Ferrari & Silveira (2015) examined the primary type specimens of both species (which are deposited at the ZMB) and found morphological differences – for instance, the shape of the hypostomal carina (refer to “Diagnosis” for more details, above) – that allow for easy differentiation. In the present study, barcoded specimens that had previously been identified as

either *C. argentinus* or *C. rugicollis* with the key provided by Ferrari & Silveira (2015) were assigned different BINs, and later placed in different clusters in the NJ analysis, thus further supporting the revalidation of *C. argentinus* proposed by those authors.

Even prior to Moure & Urban's (2002) decision to synonymize the two species, the name *C. argentinus* had been historically overlooked, especially regarding the Brazilian fauna. As a consequence, there is a great number of specimens from various bee repositories that have been misidentified as *C. rugicollis*. Therefore, some of the geographical and/or biological data that were originally attributed to *C. rugicollis* (see below) might, in fact, apply to *C. argentinus*.

*Colletes argentinus*, however, may be a junior synonym of *C. punctatissimus* Schrottky, 1902, as pointed out before by Ferrari & Silveira (2015). Several attempts to locate the male holotype of *C. punctatissimus* at the MZSP – where the specimen was indicated to be deposited (Moure & Urban 2002; Moure *et al.* 2007) – did not succeed and it may be lost (Rasmussen *et al.* 2009; Ferrari & Silveira 2015; Ramos *et al.* 2015).

While studying the type specimens of the *Colletes* species described by Vachal at the MNHP, I encountered four males of *C. argentinus* that had been labelled as syntypes. Because the collection information associated with them matched those of the type series indicated in Friese's original description of the species I have labelled them as paralectotypes.

### ***Colletes chicoi* Ferrari, new species**

(Figs. 7, 8, 9, 55A)

**Diagnosis:** The male of *C. chicoi* **n. sp.** (the female is unknown) can be diagnosed through the combination of F1 relatively short (0.8x as long as its apical width), legs mostly pale-brown, and T1 pale-brown anteriorly. It is most similar to male *C. sertanicola* **n. sp.** as they are unique in having pale legs and brownish T1–T2 discs. However, these species can be distinguished from each other by the comparatively shorter F1, 0.8x as long as its apical width, in *C. chicoi* **n. sp.** (F1 1.1x as long as its apical width in *C. sertanicola* **n. sp.**); mesoscutum densely punctate anteriorly in *C. chicoi* **n. sp.** (mesoscutum sparsely punctate anteriorly in *C. sertanicola* **n. sp.**); and T1 pale-brown anteriorly in *C. chicoi* **n. sp.** (T1 dark-brown anteriorly in *C. sertanicola* **n. sp.**).



**Figure 7.** Geographical distribution of *Colletes argentinus* (blue circles), and *C. chicoi* n. sp. (red stars). Scale bar approximately 250km.

**Description:** FEMALE: Unknown.



MALE (Figs. 8A–C):

*Dimensions (mm)*: Approximate body length 7.9; head width 2.5; head length 1.9; intertegular distance 1.7; forewing length 5.9.



**Figure 8.** *Colletes chicoi* n. sp. Male: (A) habitus, dorsal view (B); face, frontal view; (C) habitus, lateral view. Scale bars = 1mm.

*Colouration:* Black except legs (except coxae, trochanters, front tibia, mid femur, dorsal surface of front and mid tibiae dark-brown), tegula, T1 anteriorly, ventrally reflexed lateral areas of T1–T2, S1–S2, S3 anteriorly pale-brown. Mandible (except tip reddish-brown), flagellum (except ventral surface of F2–F7 pale-brown), vein R of forewing, T1–T2 discs, S3 disc dark-brown. Wing venation, stigma, tibial spurs, marginal zones of T1–T6 and S2–S5 pale-yellow.

*Structure:* Labrum medially concave; concavity margined laterally by longitudinal ridges. Clypeal mid-longitudinal area shallowly depressed throughout; depression narrowest (0.7x MOD) above, progressively broader towards lower margin (maximum breadth 2x MOD). Malar area ~1.2x as long as basal depth of mandible (39:32). Hypostomal carina short and flat. F1 ~0.8x as long as its apical width (23:28). UID:LID (54:42). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum modified as a long spine. Mesepisternum ventrally, near ventral end of episternal groove, with protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum subequal in length to metanotum (31:32); metapostnotal pits well-delimited; posterior transverse carina straight and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~4.3x longer than broad (48:11). Outer rami of hind tarsal claws ~1.3x as long as inner rami (12:9). Marginal zone of T1 flat. Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 9A, 9B, 9C, respectively.

*Pubescence:* Pale-yellow throughout. Head with plumose, erect, moderately long hairs; except mandible with moderately short setae along condylar groove; paraocular area with suberect, short hairs adjacently to inner margin of eye; interantennal, vertexal and genal areas with long hairs. Mesosoma with plumose, erect, long hairs; except pronotal lobe and scutellum with moderately long hairs; lateral surface of propodeum with very long hairs near upper margin. Legs with erect, moderately short setae; except trochanters and femora with plumose hairs; front and mid tibiae with appressed, short setae on anterodorsal surface; front and mid basitarsi with moderately long setae on posterior margin (longer on hind basitarsus). Metasomal terga and sterna covered with suberect, minute setae on discs; except T1 and S1 with plumose, erect hairs (long on T1, shorter on S1); T2 and S2 with setae and plumose hairs intermingled; T6 and S5–S6 with moderately short setae posteriorly; marginal zones of T1–T5 covered with a broad band of plumose, appressed, short hairs; marginal zones of S1–S5 with a transverse line of plumose, appressed, short hairs.

*Surface sculpture:* Clypeus densely and moderately finely punctate on mid-longitudinal depression (except sparsely punctate below); densely and finely punctate on lateral slopes and above; convex area largely impunctate; interspaces smooth throughout. Supraclypeal area densely and moderately coarsely punctate; interspaces rugulose. Malar area with coalescent, moderately coarse punctures. Paraocular area densely punctate; moderately finely punctate below, punctures slightly coarser above; interspaces smooth throughout. Frontal area punctures crowded and moderately coarse. Vertexal area densely and finely punctate; fine punctures intermingled with coarser punctures towards occipital area; interspaces smooth. Mesosomal with smooth interspaces, except when stated otherwise. Mesoscutum moderately densely and coarsely punctate (except densely and finely punctate anterolaterally and sparsely punctate posteromedially). Scutellum densely and coarsely punctate (except punctures sparse anteriorly). Metanotum densely and moderately coarsely punctate. Mesepisternum coarsely punctate; densely punctate anterior to episternal groove and below scrobe; sparsely punctate towards ventral surface. Metepisternum rugose mid-anteriorly; sparsely and moderately finely punctate above (interspaces rugulose) and below (interspaces imbricate). Lateral surface of propodeum sparsely and moderately finely punctate (except densely punctate anteriorly); interspaces imbricate. Vertical surface of metapostnotum smooth above. Metasomal terga with smooth interspaces throughout. T1 moderately densely punctate; disc with fine and moderately fine punctures intermingled. T2–T5 densely and minutely punctate (T2 with fine and minute punctures intermingled). T6 densely and finely punctate. Metasoma sterna with imbricate interspaces throughout. S1 sparsely and minutely punctate. S2–S5 moderately densely and minutely punctate (except punctures sparse mid-longitudinally). S6 sparsely and finely punctate.

**Type material:** *Holotype* ♂ – “RPSP; 17.1010”. “Brasil Pará; Cachimbo; 19 agosto 1979”. “2360”. “M.J.G Hopkins; H.C. Hopkins”. “HOLOTYPE; Colletes chicoi ♂; Ferrari, new species”. {RPSP}.

*Paratypes:* **BRAZIL – Mato Grosso:** Roadside, (-12.8333, -51.7833), 18/iii/1968, [O. Richards], 1♂, {NHMUK}. **Pará:** Serra do Cachimbo, 22/viii/1979, [Hopkins & Hopkins], 1♂, {RPSP}.

**Range:** BRAZIL (Mato Grosso and Pará). See also Fig. 7.

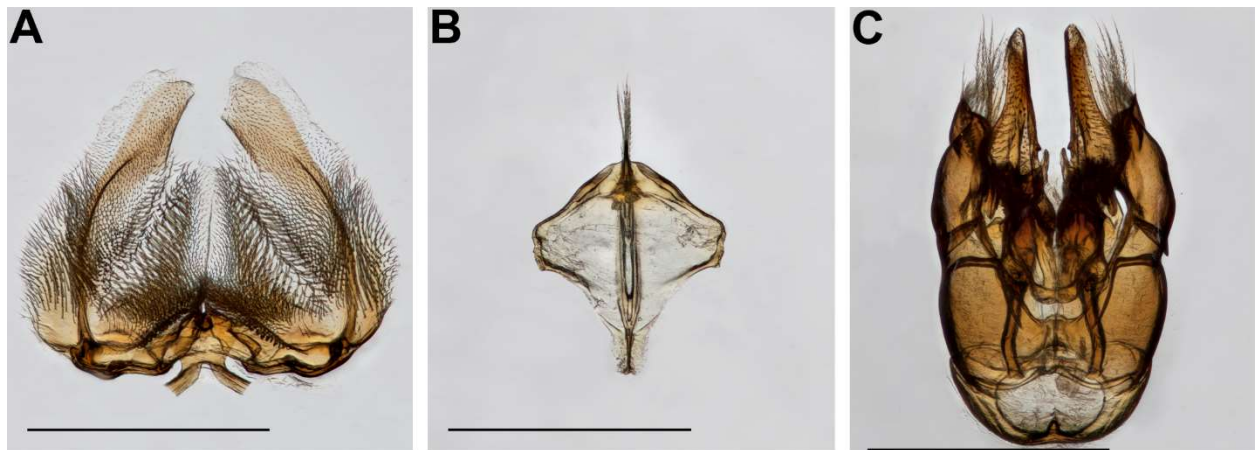
**Biogeographical distribution:** South-eastern Amazonian dominion (Xingu-Tapajós province), and Chacoan dominion (Cerrado province) at altitudes of 300–600m a.s.l.

**DNA barcode:** Unavailable.

**Floral hosts:** Unknown.

**Etymology:** This species is named in honour of Francisco Alves Mendes Filho (1944–1988), better known as Chico Mendes, a Brazilian environmentalist who dedicated his life to the conservation of the Amazon rainforest.

**Comments:** Seemingly a rare species that appears to be associated with the Amazon-Cerrado ecotone in central Brazil.



**Figure 9.** Dorsal view of the male terminalia of *Colletes chicoi* n. sp. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

***Colletes cyaneus* Holmberg, 1903**

(Figs. 10, 11, 12, 45A, 45C, 51D)

*Colletes cyaneus* Holmberg, 1903: 468; Friese 1910: 646; Jörgensen 1912b: 94; Moure 1956: 203; Schlindwein 1995: 87, 1998: 50; Moure & Urban 2002: 8; Silveira *et al.* 2002: 155; Moure *et al.* 2007: 681; Moure *et al.* 2012; Ascher & Pickering 2018.

Syntype ♀ lost. (MACN).

*Colletes semicyaneus* (= *Reedaspis semicyanea* (Spinola, 1851)); Schrottky 1907: 6.

**Diagnosis:** *Colletes cyaneus* can be diagnosed through the combination of mesoscutum with off-white and black hairs intermixed, femoral scopa of female or legs of male with off-white to pale-yellow hairs, and T1–T5 discs metallic-blue. *Colletes cyaneus* is most similar to *C.*

*michenerianus* as the two are unique amongst the species found in southern Brazil in having metallic-blue metasomal terga. Their females, however, can be differentiated from each other by labrum medially convex in *C. cyaneus* (clypeus medially concave in *C. michenerianus*); and scopa with pale-yellow hairs in *C. cyaneus* (scopa with fuscous hairs in *C. michenerianus*). The males of the two species can be distinguished by the comparatively longer malar area, ~1.8x as long as basal depth of mandible, in *C. cyaneus* (malar area ~1.5x as long as basal depth of mandible in *C. michenerianus*); and legs with off-white hairs in *C. cyaneus* (legs with fuscous hairs in *C. michenerianus*).

**Redescription:** FEMALE (Figs. 10A, 10C, 10E):

*Dimensions (mm):* Approximate body length 9.9–10.7; head width 3.6–4.0; head length 2.8–3.1; intertegular distance 3.1–3.4; forewing length 8.2–8.6.

*Colouration:* Black except metasomal terna (except T6 black) bright metallic-blue. Discs of S1–S5 metallic dark-blue. Wing venation (except veins C and R of forewing black), stigma, tibial spurs, dorsal surface of tarsi (except basitarsi black) dark-brown. Marginal zones of S1–S5 pale-yellow. Proximal 1/3 of tarsal claws pale-brown. Distal 1/3 of mandible, distal 2/3 of tarsal claws, S6 mid-longitudinally reddish-brown.

*Structure:* Labrum medially concave; concavity margined laterally by longitudinal ridges. Clypeal mid-longitudinal area narrowly (0.4x MOD) and moderately deeply depressed on upper

1/3, depression shallower and much wider below (2x MOD). Malar area ~1.1x as long as basal depth of mandible (30:27). Hypostomal carina short and flat. F1 ~1.5x as long as its apical width (46:29). UID:LID (75:76). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum pointed. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum ~0.3x as long as metanotum (11:40); metapostnotal pits well-delimited; posterior transverse carina sinuous and incomplete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~2.8x longer than broad (50:18). Outer rami of hind tarsal claws 2.8x as long as inner rami (14:5). Marginal zone of T1 flat. Marginal zone of S6 depressed.

*Pubescence:* Head with plumose, erect, long, off-white and black hairs intermixed (except mandible with fuscous, moderately long setae); clypeus with only off-white, suberect, moderately short hairs mid-longitudinally; black hairs on frontal and vertexal areas very long; genal area with suberect, short hairs near outer margin of eye. Mesosoma with plumose, erect, very long, off-white and black hairs intermixed (except mesoscutum and pronotal lobe with moderately long hairs); mesepisternum almost entirely covered with black hairs; lateral surface of propodeum with very long hairs on upper margin. Legs with pale-yellow hairs (except front trochanter with black, moderately long setae and front femur with black, long, plumose hairs); front and mid coxae with plumose, erect, moderately long, pale-yellow and fuscous hairs intermixed; mid and hind trochanters with plumose, erect, long hairs; femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; tibiae with suberect, short setae (except hind tibia with erect, long setae); basitarsi with erect, moderately long setae (except long on posterior margin of mid basitarsus, very long and posterior margin of hind basitarsus). Metasomal terga with off-white hairs (except T5–T6 discs with black, long setae); T1 with plumose, erect, long hairs; T2–T3 discs with minute, suberect setae; T4 disc with moderately short, off-white and black setae intermixed; T1–T5 marginal zones covered with appressed, short, dense hairs. Metasomal sterna with pale-yellow setae (except S1 with plumose, long hairs); S2 disc with erect, moderately short setae and branched apically only hairs intermixed; S3–S6 with suberect, short setae (except setae longer towards marginal zones); S2–S5 also with a line of plumose, moderately short hairs near marginal zones (except short on S4–S5).





**Figure 10.** *Colletes cyaneus* Holmberg, 1903. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.

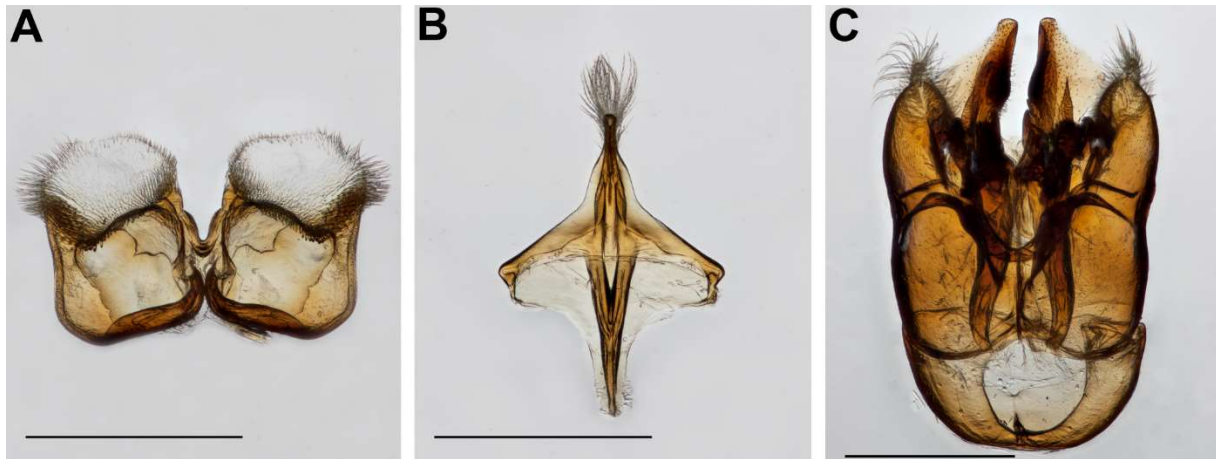
*Surface sculpture:* Clypeus longitudinally finely striate below and mid-longitudinally; punctures densest above and towards lateral slopes. Supraclypeal area largely impunctate; integument imbricate. Malar area sparsely and moderately finely punctate on upper 1/3 (interspaces smooth); longitudinally striate on lower 2/3. Paraocular area densely punctate (except sparsely punctate near upper summit of eye); moderately coarsely punctate below, slightly finer above; interspaces imbricate throughout. Frontal area punctures difficult to discern from overall rugose interspaces. Vertexal area densely and moderately finely punctate near lateral ocellus (interspaces rugulose); sparsely and finely punctate towards eye (interspaces smooth). Mesosomal interspaces imbricate (except when stated otherwise). Mesoscutum and metanotum moderately densely and moderately coarsely punctate (except sparsely punctate posteromedially). Scutellum and mesepisternum densely and coarsely punctate (except sparsely punctate on scutellar anterior surface). Metepisternum with oblique carinae mid-anteriorly; moderately densely and moderately finely punctate below; punctures above nearly indistinguishable from imbricate integument. Lateral surface of propodeum sparsely and minutely punctate. Vertical surface of metapostnotum rugose above. Metasoma with imbricate interspaces throughout. Metasomal terga minutely punctate; sparsest on T1, densest on T5. Metasomal sterna finely punctate (except S6 with moderately coarse punctures near posterior margin); S2–S4 and S6 moderately sparsely punctate (except densely punctate near marginal zones); S5 densely punctate.

MALE (Figs. 10B, 10D, 10F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.9–9.4; head width 3.3–3.5; head length 2.7–2.8; intertegular distance 2.4–2.6; forewing length 7.6–7.9.

*Colouration:* Dorsal surface of distitarsi pale-brown. T5 with metallic-blue and greenish-blue reflections. Marginal zones of S1–S5 dark-brown.

*Structure:* Labrum medially convex; convexity not margined laterally by longitudinal ridges. Clypeal mid-longitudinal depression broader (0.8x MOD) above. Malar area ~1.8x as long as basal depth of mandible (35:20). F1 ~1.2x as long as its apical width (34:28). UID:LID (72:67). Hind basitarsus ~3.2x longer than broad (54:17). Outer rami of hind tarsal claws 1.6x as long as inner rami (16:10). S7, S8 and genital capsule as in Figs. 11A, 11B, 11C, respectively.



**Figure 11.** Dorsal view of the male terminalia of *Colletes cyaneus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Pubescence:* Mandible with pale-yellow setae. Clypeal lateral slopes, interantennal area, pronotal lobe, mesepisternum, metepisternum, lateral surface of propodeum, legs with only off-white hairs. Genal area near outer margin of eye with erect hairs. Frontal trochanter with plumose hairs. Legs with off-white hairs; front and mid tibiae with moderately long setae. Disc of T2 with setae and plumose hairs intermixed.

*Surface sculpture:* Clypeus striate only below; clypeal mid-longitudinal depression densely punctate. Malar area longitudinally striate throughout. Lower paraocular area and scutellum anteriorly with smooth interspaces. Mesepisternum moderately densely and moderately coarsely punctate. T2–T6 finely punctate. S2–S5 densely punctate. S6 finely punctate throughout.

**Material studied:** BRAZIL – Rio Grande do Sul: 10.5km SW of Pinheiro Machado, (-31.6366, -53.4536), 2/xi/2012, [Almeida & Aguiar], 1♀, {RPSP}. 12km NNE of Pedras Altas, (-31.6566, -53.5377), 2/xi/2012, [Almeida & Aguiar], 1♀5♂♂, {RPSP}; idem, except 5/xi/2012, 1♀. 39km NE of Bagé, (-30.8708, -53.6163), 1/xi/2012, [Almeida & Aguiar], 1♀, {RPSP}. Caçapava do Sul, Guaritas, 1/x/1992, [C. Schlindwein], 2♀♀, {UFMG}; idem, except 15/x/1992, 1♂; idem, except 11/x/1993, 1♂. Santana do Livramento, (-30.8730, -55.5283), 3/xi/2012, [Almeida & Aguiar], 2♀♀, {RPSP}.

**Range:** ARGENTINA (Buenos Aires), BRAZIL (Rio Grande do Sul). See also Fig. 12.





**Figure 12.** Geographical distribution of *Colletes cyaneus* (green circles), *C. flagellaris* **n. sp.** (red diamond), and *C. sertanicola* **n. sp.** (blue star). Scale bar approximately 250km.

**Biogeographical distribution:** Chacoan dominion (Pampean province) at altitudes of 0–500m a.s.l.

**DNA barcode:** Available. BOLD: ADI1118 (1♀1♂). Distance from the nearest neighbour (*C. musculus* Friese, 1910): 3.36–4.55%.

**Floral hosts:** According to Schlindwein (1995, 1998), *C. cyaneus* visits the following plant species: Anacardiaceae – *Schinus molle* L. Berberidaceae – *Berberis laurina* Thunb. Lamiaceae – *Glechon thymoides* Spreng. Leguminosae – *Adesmia riograndensis* Miotto. Loasaceae – *Blumenbachia insignis* Schrad. Polygalaceae – *Monnina cuenata* A. St.-Hil.

**Comments:** Uncommon species seemingly endemic to the South American Pampas.

The female syntype of *C. cyaneus* that was originally deposited at the MACN is lost (A. Roig-Alsina, *pers. comm.*). Thus, final decision on the species' identity was made based upon examination of photographs of the female specimen that will be designated as the neotype in a different study (Roig-Alsina *et al.*, *in prep.*). This specimen, which is currently deposited at the MACN, is labelled as follows: “Buenos Aires; Hurlingham, INTA; Castelar. 6-XI-2003; Compagnucci Roig Alsina”. “*Colletes cyaneus* ♀; Holmberg; NEOTYPUS; Ferrari, Compagnucci; & Roig Alsina”.

*Colletes cyaneus* was incorrectly placed under synonymy with *C. semicyaneus* (= *Reedapis semicyanea*), a member of Neopasiphaeinae, by Schrottky (1907).

### ***Colletes ferenudus* Ferrari, new species**

(Figs. 13, 14, 49A, 50A)

**Diagnosis:** The combination of mesoscutum with pale-orange hairs, mesepisternum with imbricate interspaces, and T2–T5 covered with sparse black short setae is sufficient to diagnose *C. ferenudus* **n. sp.** This species is most similar to *C. kerri* as in their females (the male of *C. ferenudus* **n. sp.** is unknown) the mesoscutum has pale-orange hairs and T2–T5 are not covered with dense appressed hairs. However, the two species can be distinguished from one another by clypeus striate only below in *C. ferenudus* **n. sp.** (clypeus striate throughout in *C. kerri*); and mesepisternum with imbricate interspaces in *C. ferenudus* **n. sp.** (mesepisternum with smooth interspaces in *C. kerri*).





**Figure 13.** *Colletes ferenudus* n. sp. Female: (A) habitus, dorsal view (B); face, frontal view; (C) habitus, lateral view. Scale bars = 1mm.



**Description:** FEMALE (Figs. 13A–C):

*Dimensions (mm):* Approximate body length 11.2; head width 3.6; head length 2.6; intertegular distance 3.1; forewing length 8.6.

*Colouration:* Black except distal half of mandible, distal 1/3 of tarsal claws reddish-brown. Ventral surface of F2–F9 dark-orange. Tegula, wing venation (except veins C and R of forewing black), proximal 1/3 of tarsal claws pale-brown. Tibial spurs, dorsal surface of distitarsi, marginal zones of T1–T5 dark-brown. Marginal zones of S1–S5 pale-yellow.

*Structure:* Labrum medially concave; concavity not margined laterally by longitudinal ridges. Clypeal mid-longitudinal area shallowly depressed on lower 3/4; depression moderately broad (0.8x MOD) above, much broader (1.9x MOD) towards lower margin. Malar area ~0.9x as long as basal depth of mandible (41:46). Hypostomal carina short and flat. F1 1.5x as long as its apical width (42:28). UID:LID (69:65). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum rounded. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum ~0.5x as long as metanotum (20:41); metapostnotal pits well-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa with weak spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.8x longer than broad (68:18). Outer rami of hind tarsal claws 2.8x as long as inner rami (14:5). Marginal zone of T1 flat. Marginal zone of S6 not depressed.

*Pubescence:* Head with plumose, erect, moderately long, off-white and black hairs intermixed; except mandible with pale-yellow setae on lower margin; interantennal, upper paraocular, vertexal and genal (towards proboscidal fossa) areas with long hairs. Mesosoma with pale-orange, plumose, erect, long hairs; except pronotal lobe and mesoscutum with moderately long hairs, upper margin of lateral surface of propodeum with very long hairs; mesepisternum and metepisternum with pale-yellow and fuscous hairs intermixed; lateral surface of propodeum with pale-yellow, appressed, short hairs on disc. Legs with fuscous hairs (except mid and hind trochanters and femora with off-white hairs and hind tarsus with pale-yellow setae on posterior margin); trochanters and femora with plumose, erect, long hairs; femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; mid and hind tibiae with suberect, short setae (except posterior surface with erect setae); tarsi and hind tibia with erect, moderately long setae (except hind tarsus with long setae on posterior margin). T1 with pale-

yellow, plumose, erect, long hairs (those hairs suberect, moderately long laterally); T2–T5 with pale-yellow, suberect, moderately short setae on discs; discs of T2–T4 also with off-white, sparse, plumose, appressed, very short hairs; T6 with black, suberect, moderately short setae. S1 with pale-yellow, plumose, erect, moderately long hairs; S2 with fuscous, branched apically only, erect, moderately short hairs on disc; S3–S6 with pale-yellow, erect, short setae on discs (except S5 with moderately long setae laterally); S2–S5 marginal zones with plumose, suberect, short hairs.

*Surface sculpture:* Clypeus sparsely and moderately coarsely punctate (except lateral slopes densely and moderately finely punctate); interspaces imbricate; lower 1/3 longitudinally striate medially. Supraclypeal area imbricate. Malar area substrigulate. Paraocular area moderately finely punctate (except finely punctate near clypeus); densely punctate below, sparser above (punctures limits somewhat ill-defined), sparsest towards antennal socket; interspaces imbricate throughout. Frontal area rugose. Vertexal area sparsely and finely punctate (except densely punctate adjacently to occipital area); interspaces rugulose. Mesoscutum moderately coarsely punctate; punctures dense laterally, sparser anteriorly, sparsest posteromedially; interspaces Scutellum densely and moderately coarsely punctate (except punctures sparse anteriorly and crowded posteriorly); interspaces imbricate. Metanotum moderately densely and moderately coarsely punctate; interspaces imbricate. Mesepisternum moderately densely and moderately coarsely punctate (except densely punctate anterior to episternal groove and towards metepisternum); interspaces imbricate. Metepisternum with oblique carinae anteriorly; punctures difficult to discern from microareolate interspaces above and below. Lateral surface of propodeum moderately sparsely and moderately finely punctate; interspaces imbricate. Vertical surface of metapostnotum rugose above. Metasomal terga sparsely and minutely punctate (except T6 densely and moderately finely punctate); interspaces imbricate (except T1 disc smooth). Metasomal sterna with imbricate interspaces throughout; S1–S2 sparsely and finely punctate (except S1 minutely punctate posterolaterally); S3–S4 sparsely and minutely punctate; S5 moderately densely and finely punctate; S6 densely and finely punctate mid-longitudinally, sparsely and moderately finely punctate laterally.

MALE: Unknown.

**Type material:** *Holotype* ♀ – “RPSP; 12.3948”. “Brasil, RS, Santana do; Livramento. 30°52'23"S; 55°31'42"W, 200m. 03.xi.2012; E. Almeida & A. Aguiar, cols”. “CCDB-30344 E5”. “HOLOTYPE; *Colletes ferenudus* ♀; Ferrari, new species”. {RPSP}.

**Paratypes:** **BRAZIL – Paraná:** Guarapuava, 8/ix/1955, [C. Michener], 1♀, {SEMC}. **Rio Grande do Sul:** 12km NNE of Pedras Altas, (-31.6566, -53.5377), 2/xi/2012, [Almeida & Aguiar], 1♀, {RPSP}. Caçapava do Sul, Minas do Camaquã, 27/x/2009, [Schlindwein], 1♀, {UFMG}. Santana do Livramento, (-30.8730, -55.5283), 3/xi/2012, [Almeida & Aguiar], 4♀♀, {RPSP}.

**Range:** BRAZIL (Paraná, Rio Grande do Sul). See also Fig. 14.

**Biogeographical distribution:** Chacoan dominion (Pampean province), and Parana dominion (*Araucaria* Forest province) at altitudes of 0–500m a.s.l.

**DNA barcode:** Available. BOLD: ACV1831 (4♀♀). Distance from the nearest neighbour (*C. distinctus* Cresson, 1868): 8.10–8.27%.

**Floral hosts:** Loasaceae – *Blumenbachia insignis* Schrad.

**Etymology:** From the Latin words “fere” (nearly) and “nudum” (bare) in allusion to the species’ metasoma that is very sparsely hairy.

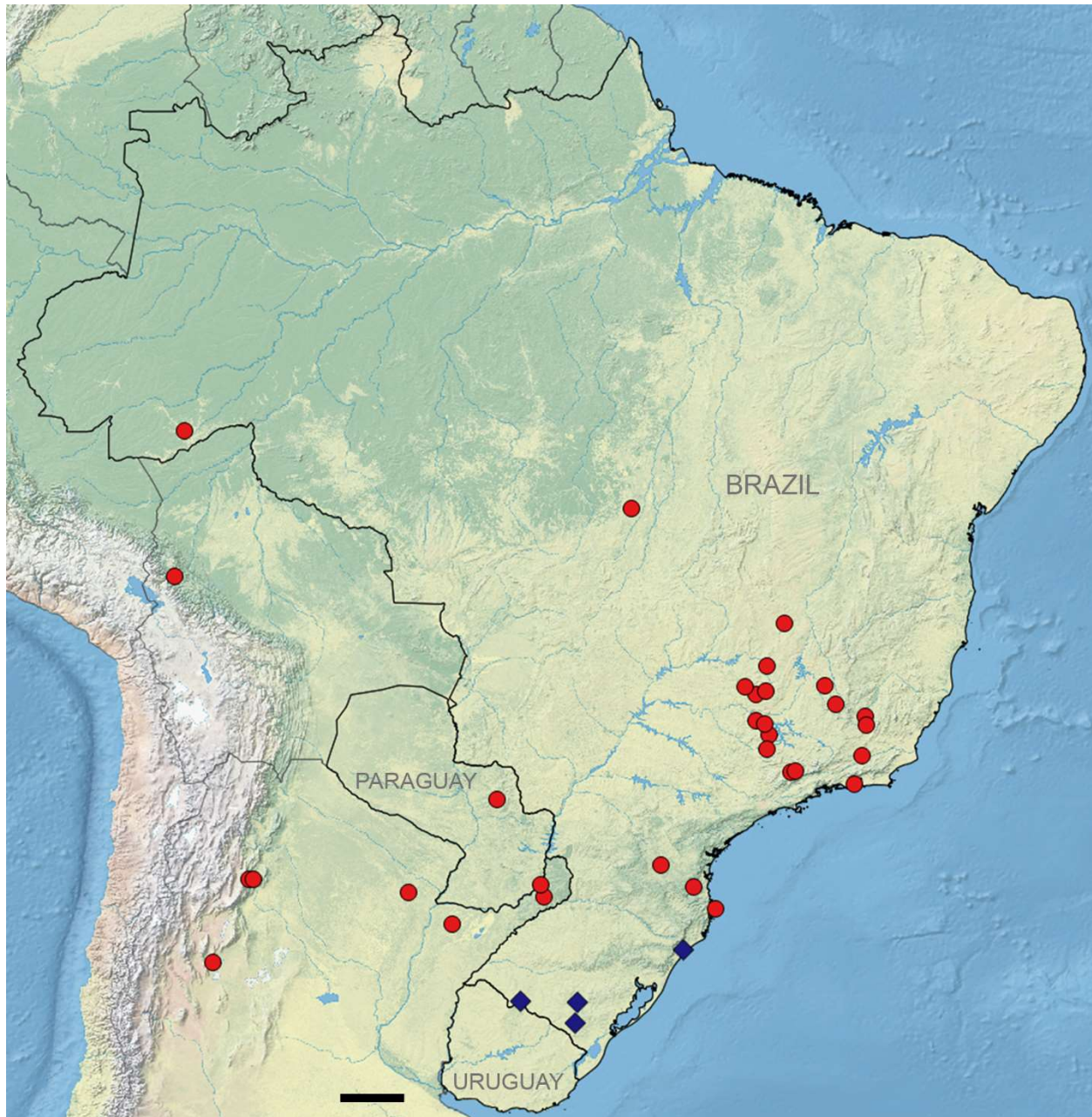
**Comments:** Apparently a rare species which is only known from southern Brazil.

### ***Colletes flagellaris* Ferrari, new species**

(Figs. 12, 15, 16, 51A)

**Diagnosis:** Both sexes of *C. flagellaris* **n. sp.** can be diagnosed through the combination of labrum black, flat and without ridges; mesosoma with pale-orange hairs; and T2–T5 covered with pale-yellow, short, appressed hairs. *Colletes flagellaris* **n. sp.** is most similar to *C. rufipes* as both have labrum flat, and T2–T5 covered with appressed hairs. However, these species can be

differentiated from each other by labrum black in *C. flagellaris* **n. sp.** (labrum reddish-brown in *C. rufipes*); F1 relatively long, 1.9/1.3x (♀/♂) as long as its apical width, in *C. flagellaris* **n. sp.** (F1 1.4/1.1x (♀/♂) as long as its apical width in *C. rufipes*); and legs black in *C. flagellaris* **n. sp.** (legs dark-orange in *C. rufipes*).



**Figure 14.** Geographical distribution of *Colletes ferenudus* **n. sp.** (blue diamonds), and *C. petropolitanus* (red circles). Scale bar approximately 250km.

**Description:** FEMALE (Figs. 15A, 15C, 15E):

*Dimensions (mm):* Approximate body length 10.3; head width 3.7; head length 3.0; intertegular distance 2.9; forewing length 8.4.

*Colouration:* Black except distal half of mandible, S6 posteriorly reddish brown. Ventral surface of F2–F10, dorsal surface of distitarsi, ventrally reflexed lateral area of T1, S2–S5 mid-longitudinally and posteriorly dark-brown. Tegula, wing venation (except forewing veins C, R1, 2r-m and 2m-cu pale-brown and vein R black), tarsal claws (except proximal half pale-brown) pale-orange. Tibial spurs, marginal zones of S1–S5 pale-yellow.

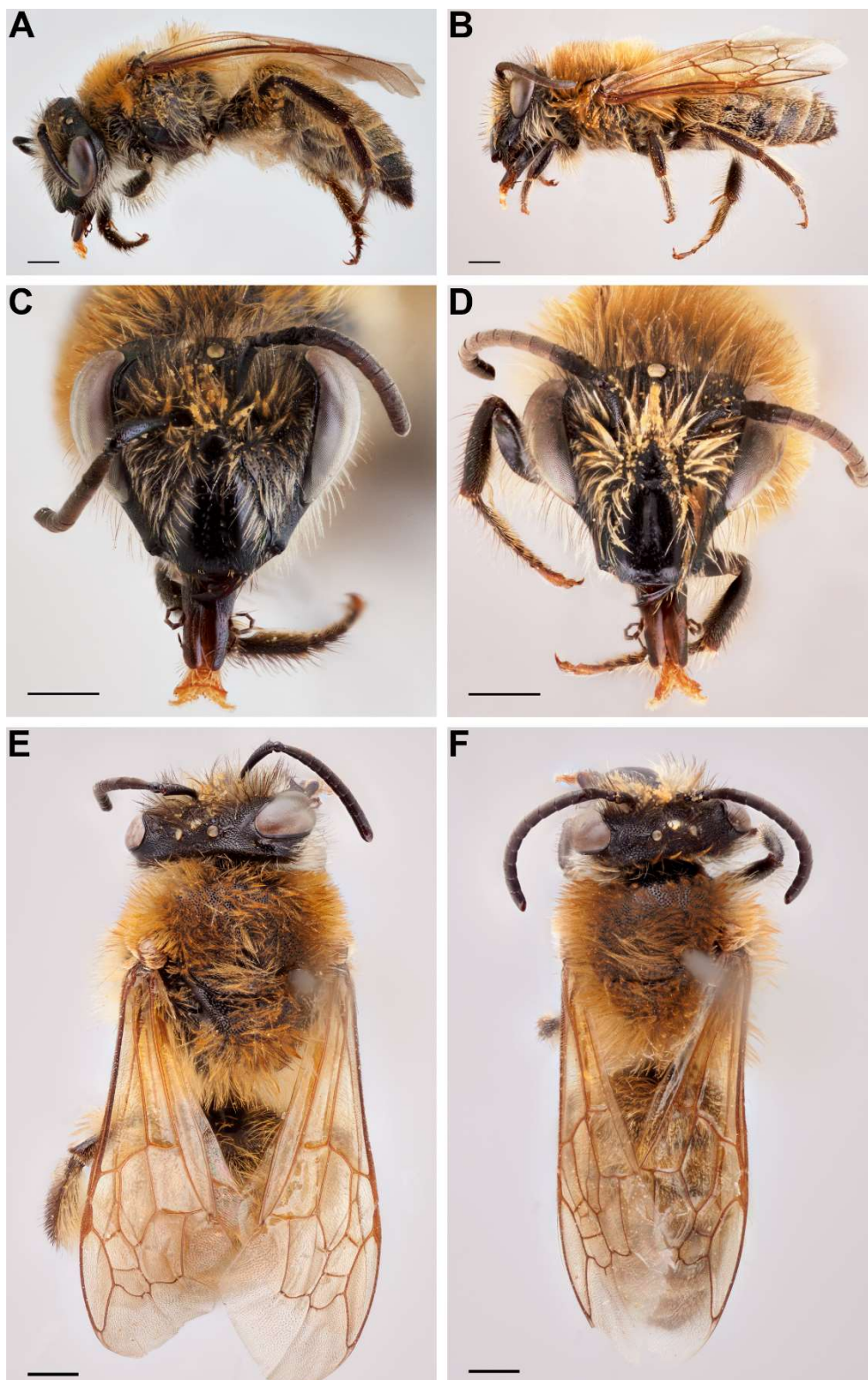
*Structure:* Labrum medially flat and lacking longitudinal ridges. Clypeal mid-longitudinal area very shallowly depressed throughout; depression relatively narrow (0.6x MOD) above; depression progressively broader (maximum width 1.4x MOD) towards lower margin. Malar area 1.4x as long as basal depth of mandible (49:35). Hypostomal carina short and flat. F1 ~1.9x as long as its apical width (37:20). UID:LID (73:67). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum pointed. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum ~0.6x as long as metanotum (32:54); metapostnotal pits well-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.3x longer than broad (56:17). Outer rami of hind tarsal claws ~4.2x as long as inner rami (17:4). Marginal zone of T1 flat. Marginal zone of S6 not depressed.

*Pubescence:* Head with pale-yellow, plumose, erect, moderately long hairs; except mandible with moderately long setae; clypeal lateral slopes and lower paraocular area with suberect hairs; paraocular, vertexal and frontal areas with pale-yellow and black hairs intermixed; vertexal area with black, long hairs near occipital hairs; genal area with off-white and fuscous hairs intermixed adjacently to outer margin of eye and very long hairs towards proboscideal area. Mesosoma with pale-orange, plumose, erect, long hairs; except those hairs shorter on mesoscutum, shortest on pronotal lobe; pronotal lobe, mesoscutal disc, scutellum and metanotum anteriorly with pale-orange and fuscous hairs intermixed; lateral surface of propodeum with appressed, moderately short hairs posteriorly and erect, very long hairs on upper margin. Legs with pale-yellow, erect, long hairs on trochanters and femur (except front femur

with pale-yellow and fuscous hairs intermixed ventrally); femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; tibiae with fuscous, erect, moderately long setae (except front tibia with suberect, short setae dorsally and hind tibia with pale-yellow setae ventrally); basitarsi with fuscous, erect, moderately short setae (those setae pale-yellow on ventral surfaces and long on posterior margins). Metasoma terga (except T6) covered with bright-yellow, plumose, appressed, short hairs; T1 also with pale-yellow, plumose, erect, long hairs on disc; those hairs short on T2; T3–T5 also with black, erect, short setae (those setae moderately long laterally); T6 covered with black, suberect, moderately short setae throughout. Metasomal sterna with pale-yellow hairs (except S5 posteriorly and S6 with fuscous hairs); S1–S2 with plumose, erect, moderately long hairs; S3–S5 discs with erect, short setae (except S5 with moderately short setae posteriorly); S2–S4 marginal zones with a transverse line of plumose, suberect, moderately short hairs; S6 with erect, short setae distributed mid-longitudinally.

*Surface sculpture:* Clypeus sparsely and moderately finely punctate (except mid-longitudinal depression moderately densely punctate); interspaces smooth (except substrigulate below). Supraclypeal area imbricate. Malar area longitudinally finely striate on upper 3/4, substrigulate on lower 1/4. Paraocular area densely and moderately finely punctate (except punctures crowded and fine near eye and coarse towards clypeus); interspaces smooth below, imbricate above. Frontal area densely and moderately coarsely punctate; interspaces imbricate. Vertexal area densely and moderately finely punctate near lateral ocellus; those punctures sparser and intermingled with minute punctures near eye; interspaces smooth. Mesoscutum densely and moderately coarsely punctate (except punctures moderately dense and coarse posteromedially); interspaces smooth. Scutellum densely and coarsely punctate (except punctures crowded laterally and posteriorly); interspaces smooth (except rugulose posteriorly). Metanotum punctures crowded and moderately coarse. Mesepisternum densely and coarsely punctate anteriorly do episternal groove and below scrobe; sparsely and moderately coarsely towards ventral surface; interspaces smooth. Metepisternum with oblique carinae mid-anteriorly; rugose above; densely and moderately coarsely punctate below (interspaces rugulose). Lateral surface of propodeum sparsely and moderately finely punctate (except densely punctate above and posteriorly); interspaces smooth. Vertical surface of metapostnotum rugose above. Metasomal terga with smooth interspaces throughout. T1–T5 sparsely and minutely punctate.





**Figure 15.** *Colletes flagellaris* n. sp. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.

T6 moderately densely and finely punctate. Metasomal sterna with imbricate interspaces (except S6 rugulose posteriorly). S1–S4 finely punctate; S1 sparsely punctate throughout, S2–S4 moderately densely punctate (except punctures sparse mid-longitudinally). S5 more evenly densely punctate. S6 densely and moderately coarsely punctate (except punctures minute mid-longitudinally); punctures poorly defined posterolaterally.

MALE (Figs. 15B, 15D, 15F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 9.1; head width 3.4; head length 2.8; intertegular distance 2.6; forewing length 7.5.

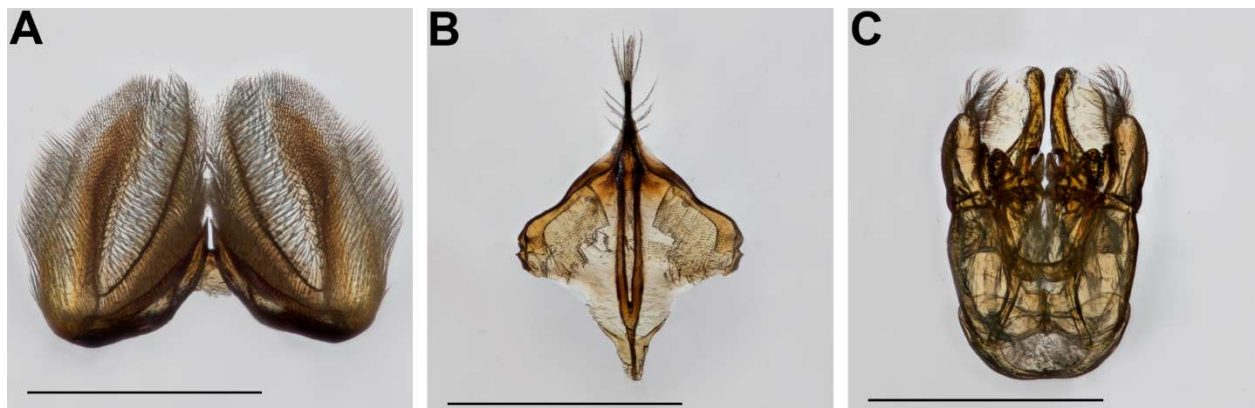
*Colouration*: Reddish-brown spot on mandible restricted to distal 1/3. Ventral surface of F3–F6 dark-orange. Distal ring of tibiae and dorsal surface of tarsi dark-brown (except dorsal surface of distitarsi pale-brown). Marginal zones of T1–T6 pale-yellow. S2–S5 mid-longitudinally black. S6 entirely black.

*Structure*: Clypeal mid-longitudinal area very deeply and relatively narrowly (0.7x MOD) depressed above; depression much shallower and broader (1.3x MOD) below. Malar area ~2.5x as long as basal depth of mandible (51:20). F1 1.3x as long as its apical width (26:20). UID:LID (72:60). Horizontal surface of metapostnotum ~0.5x as long as metanotum (19:36); posterior transverse carina incomplete. Hind basitarsus ~3.9x longer than broad (47:12). Outer rami of hind tarsal claws 2.1x as long as inner rami (21:10). S7, S8 and genital capsule as in Figs. 16A, 16B, 16C, respectively.

*Pubescence*: Paraocular area with erect hairs only. Vertexal area with black, very long hairs throughout. Mesosomal fulvous hairs restricted to mesoscutum. Pronotal lobe and mesoscutum hairs as long as those of scutellum. Lateral surface of propodeum with only erect hairs throughout. Basitarsi with pale-yellow setae. Setae on T4–T5 discs and laterally evenly long. T6 with pale-yellow, plumose, appressed, short hairs amongst fuscous, erect, moderately short setae. S3 disc with plumose hairs and setae intermixed. S5 setae pale-yellow throughout. S6 with plumose hairs posteromedially; setae evenly distributed on disc.

*Surface sculpture*: Clypeus finely punctate; interspaces smooth (except substrigulate lower-laterally). Supraclypeal area densely and moderately coarsely punctate. Paraocular area evenly densely punctate. Frontal area punctures crowded. Vertexal area punctures crowded and

moderately fine throughout. Lateral surface of propodeum moderately densely punctate centrally; interspaces imbricate. T1 densely and moderately finely punctate. T2–T3 densely and finely punctate. S2 sparsely punctate. S4–S5 minutely punctate anteriorly; punctures coarse towards marginal zones. S6 moderately densely and finely punctate on disc; punctures coarse posteriorly.



**Figure 16.** Dorsal view of the male terminalia of *Colletes flagellaris* n. sp. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Type material:** *Holotype* ♀ – “Abelhas Altimontanas; ParNa do Itatiaia; 12841-37950”. “Itatiaia RJ; BRASIL 16/03/2007; A. A. Azevedo”. “*Colletes rufipes* ♀; Smith, 1879; R.R.Ferrari, det. 2011”. “CCDB-22009; E05”. “HOLOTYPE; *Colletes flagellaris* ♀; Ferrari, new species”. {UFMG}.

*Paratypes:* **BRAZIL – Rio de Janeiro:** Itatiaia, Parque Nacional do Itatiaia, 16/iii/2007, [A. Azevedo], 3♂♂, {UFMG}.

**Range:** BRAZIL (Rio de Janeiro). See also Fig. 12.

**Biogeographical distribution:** Paraná dominion (Atlantic forest province). Species seemingly associated with the Mantiqueira mountain range (southeastern Brazil) which highest point is located at 2798m a.s.l.

**DNA barcode:** A non-BIN-compliant sequence (248 bp) is available for one male specimen (CCDB-30383-D07).

**Floral hosts:** Unknown.

**Etymology:** Allusion to the fact that this species possesses very long F1.

**Comments:** Apparently a rare species.

The type series of *C. flagellaris* **n. sp.** had been misidentified as *C. rufipes* by me for the purpose of a previous study (Ferrari & Silveira 2015). The two species are remarkably similar to each other, but they can be reasonably easily differentiated by the characters given at “Diagnosis” (above) and key (below).

***Colletes furfuraceus* Holmberg, 1886**

(Figs. 17, 18, 19)

*Colletes furfuracea* Holmberg, 1886: 183.

Holotype ♀ lost. (MACN).

*Colletes furfuraceus*; Dalla Torre 1896: 41; Friese 1906: 89, 1908:10, 1910: 650, 1912: 367, 1916: 290; Schrottky 1907: 5, 1913: 236; Jensen-Haarup 1908: 100; Jörgensen 1909: 55, 1912a: 300, 1912b: 96; Graf 1968: 73; Moure & Urban 2002: 10; Silveira *et al.* 2002: 155; Moure *et al.* 2007: 681; Almeida & Danforth 2009: 293; Kuhlmann *et al.* 2009: 296; Moure *et al.* 2012; Ascher & Pickering 2018.

*Colletes furfuracens* (sic); Schrottky: 1903: 180.

*Colletes furfurasceus* (sic); Schlindwein 1995: 88, 1998: 51.

**Diagnosis:** The female of *C. furfuraceus* can be diagnosed through the combination of clypeus longitudinally striate, labrum with mid depression margined laterally by longitudinal ridges, and metasoma terga (except T6) covered with pale-yellow appressed hairs. The male is diagnosable by the combination of malar area longer than basal depth of mandible, paraocular area with only pale hairs, and T3–T5 discs back and covered with short setae. *Colletes furfuraceus* is most

similar to *C. sexangulus* **n. sp.** as in their females (the male of the latter is unknown) the labrum is concave mid-longitudinally and the concavity is margined by lateral ridges, F1 is roughly 1.5x as long as its apical width, and T1–T5 are covered with pale-yellow appressed hairs. However, they can be distinguished from each other by malar area relatively long (~1.2x MOD) in *C. furfuraceus* (malar area 0.8x MOD in *C. sexangulus* **n. sp.**); dorsolateral angle of pronotum modified into a long spine in *C. furfuraceus* (dorsolateral angle of pronotum only pointed in *C. sexangulus* **n. sp.**); and T1–T5 with dark-brown marginal zones in *C. furfuraceus* (T1–T5 marginal zones pale-yellow in *C. sexangulus* **n. sp.**).

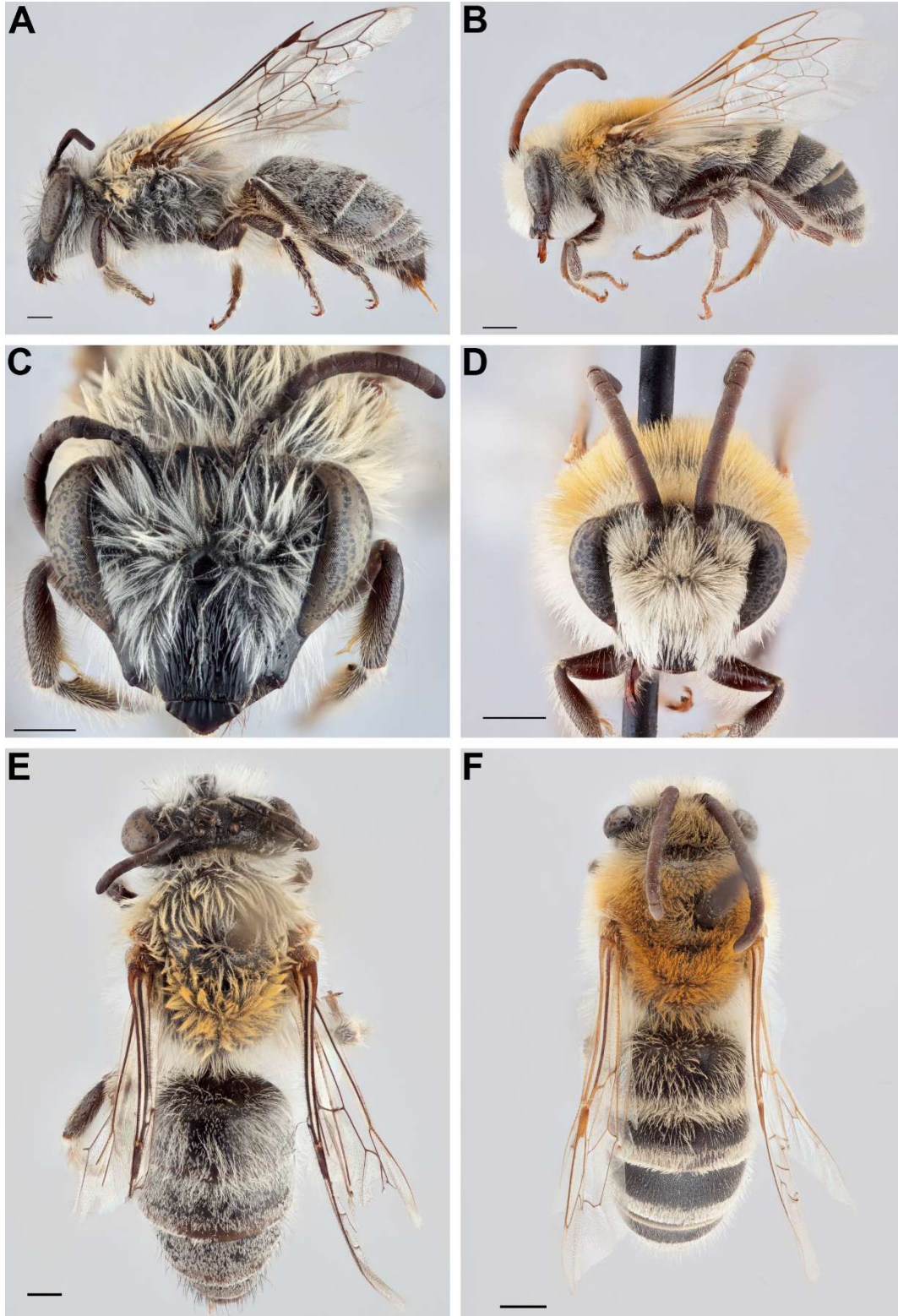
**Redescription:** FEMALE (Figs. 17A, 17C, 17E):

*Dimensions (mm):* Approximate body length 9.6–10; head width 3.2–3.4; head length 2.6–2.7; intertegular distance 2.5–2.8; forewing length 7.1–7.4.

*Colouration:* Black except distal 1/3 of mandible, distal 2/3 of tarsal claws reddish-brown. Ventral surface of F2–F10, wing venation (except vein R black), stigma, anterodorsal surface of mid femur, distitarsi, ventrally inflexed lateral area of T1, marginal zones of T1–T5, disc of S2, mid-longitudinal area of S6 dark-brown. Tegula, proximal 1/3 of tarsal claws pale-brown. Tibial spurs, marginal zones of metasomal sterna pale-yellow.

*Structure:* Labrum medially concave; concavity margined laterally by longitudinal ridges. Clypeal mid-longitudinal area deeply depressed; depression moderately broad (0.7x MOD) above, slightly narrower (0.5x MOD) below. Malar area 1.25x as long as basal depth of mandible (50:40). Hypostomal carina short and flat. F1 1.5x as long as its apical width (36:24). UID:LID (67:62). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum modified into a long spine. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum ~0.3x as long as metanotum (18:52); metapostnotal pits well-delimited; posterior transverse carina straight and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.6x longer than broad (59:16). Outer rami of hind tarsal claws 2x as long as inner rami (14:7). Marginal zone of T1 flat. Marginal zone of S6 depressed.





**Figure 17.** *Colletes furfuraceus* Holmberg, 1886. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.



*Pubescence:* Head with off-white, plumose, erect, long hairs; except mandible with fuscous setae; paraocular, frontal and vertexal areas with off-white and black hairs intermixed; genal area with suberect, moderately short hairs adjacently to outer margin of eye; proboscoidal fossa with very long hairs. Mesosoma with pale-yellow, plumose, erect, long hairs; except pronotal lobe with moderately short hairs; mesepisternum and metepisternum with off-white hairs; lateral surface of propodeum with off-white, plumose, appressed, short hairs on disc. Legs with pale-yellow, erect, moderately long setae; except trochanters and femora with plumose, long hairs anteroventrally; front tibia with suberect, short setae anterodorsally; mid and hind tibiae with fulvous setae posteriorly; femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; mid and hind basitarsi with long setae posteriorly. Metasoma terga covered with pale-yellow, plumose, appressed, short hairs (except T6 with black, suberect, moderately short setae); T1 with plumose, erect, long hairs; T2–T3 with pale-yellow, erect, short setae; T4–T5 with black, erect, long setae. Metasomal sterna with pale-yellow hairs (except S6 with fuscous setae posteriorly); S1 with plumose, erect, moderately long hairs; S2 disc with branched apically only, erect, moderately long hairs; S3–S6 discs with erect, moderately short setae (those setae longer on S5 posteriorly); marginal zones of S2–S4 with a transverse line of plumose, suberect hairs.

*Surface sculpture:* Clypeal convex area longitudinally striate; mid-longitudinal depression sparsely and moderately finely punctate; integument smooth throughout. Supraclypeal area imbricate. Malar area sparsely and moderately finely punctate; interspaces rather finely striate. Paraocular area densely punctate; punctures moderately coarse below, finer above; interspaces smooth throughout. Frontal area densely and moderately coarsely punctate; interspaces imbricate. Vertexal area sparsely and finely punctate near eye; punctures denser and coarser towards lateral ocellus; interspaces smooth throughout. Mesoscutum moderately densely and moderately coarsely punctate (except sparsely punctate posteromedially); interspaces smooth. Scutellum densely and moderately coarsely punctate (except punctures sparser anteriorly and finer posteriorly); interspaces smooth. Metanotum punctures crowded and moderately fine. Mesepisternum densely and coarsely punctate; interspaces rugulose anterior to episternal groove, smooth elsewhere. Metepisternum with oblique carinae mid-anteriorly; rugose above; densely and moderately finely punctate below. Lateral surface of propodeum sparsely and moderately finely punctate; interspaces rugulose. Vertical surface of metapostnotum with

transverse carinae above. Metasoma terga with smooth interspaces; T1 sparsely and finely punctate; T2–T5 minutely punctate. Metasomal sterna with imbricate interspaces; S2–S5 sparsely and moderately finely punctate; S6 densely and moderately coarsely punctate (except finely punctate anteriorly).

MALE (Figs. 17B, 17D, 17F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 8.7–9.3; head width 2.9–3.2; head length 2.3–2.5; intertegular distance 2.3–2.6; forewing length 7.0–7.5.

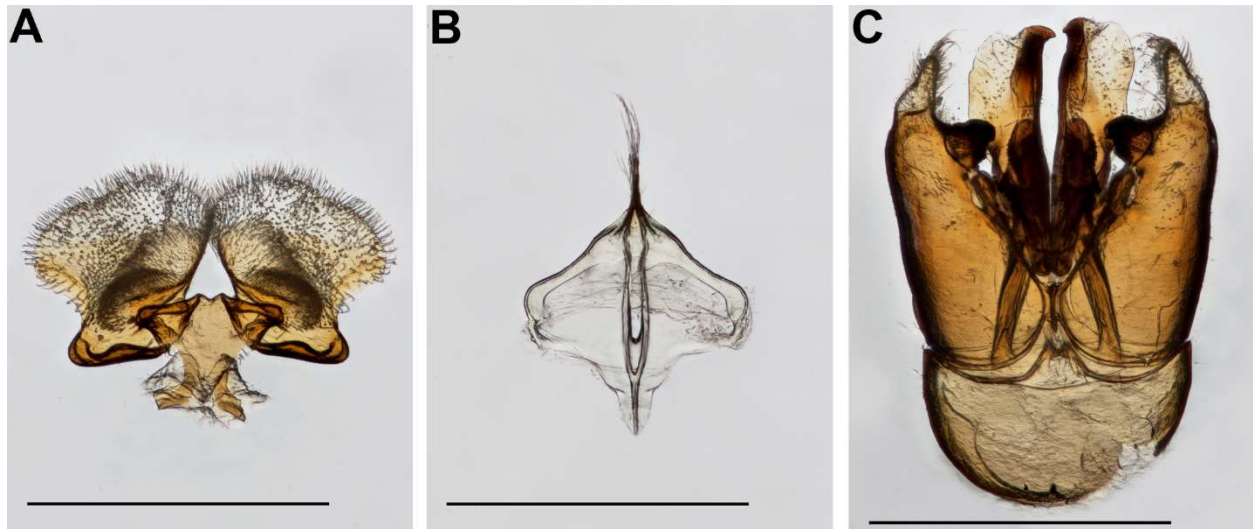
*Colouration*: Ventral surface of F2–F5 pale-brown. Dorsal surface of mediotarsi pale-brown. Wing venation and stigma pale-yellow.

*Structure*: Labral mid concavity not margined laterally by longitudinal ridges. Clypeal mid-longitudinal area shallowly depressed; depression narrow (0.3x MOD) above, much broader (maximum width 1.8x MOD) below. Malar area ~1.2x as long as basal depth of mandible (39:33). F1 ~0.9x as long as its apical width (23:25). UID:LID (64:52). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum pointed. Horizontal surface of metapostnotum ~0.6x as long as metanotum (22:39); metapostnotal pits well-delimited; posterior transverse carina complete. Hind basitarsus 4.1x longer than broad (41:10). Outer rami of hind tarsal claws 1.9x as long as inner rami (19:10). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 18A, 18B, 18C, respectively.

*Pubescence*: Mandible with plumose hairs. Genal area with erect hairs throughout. Pronotal lobe hairs as long as those of mesoscutum. Lateral surface of propodeum with erect, very long hairs on disc. T1–T5 with appressed, short hairs restricted to marginal zones. T2 disc with plumose, erect, moderately long hairs. T6 with pale-yellow setae. S2 disc with plumose hairs. Setae on S3–S5 discs with evenly long setae. S6 with pale-yellow setae throughout.

*Surface sculpture*: Clypeal convex area moderately coarsely punctate; mid-longitudinal depression with punctures crowded and fine. Supraclypeal area with crowded punctures. Malar not striate. Paraocular area punctures crowded and fine below. Vertexal area densely and moderately finely punctate throughout. Mesoscutum densely punctate posteromedially.

Metanotum densely punctate. T1 moderately densely and moderately finely punctate. T2–T5 densely and finely punctate. S5–S6 sparsely and finely punctate.



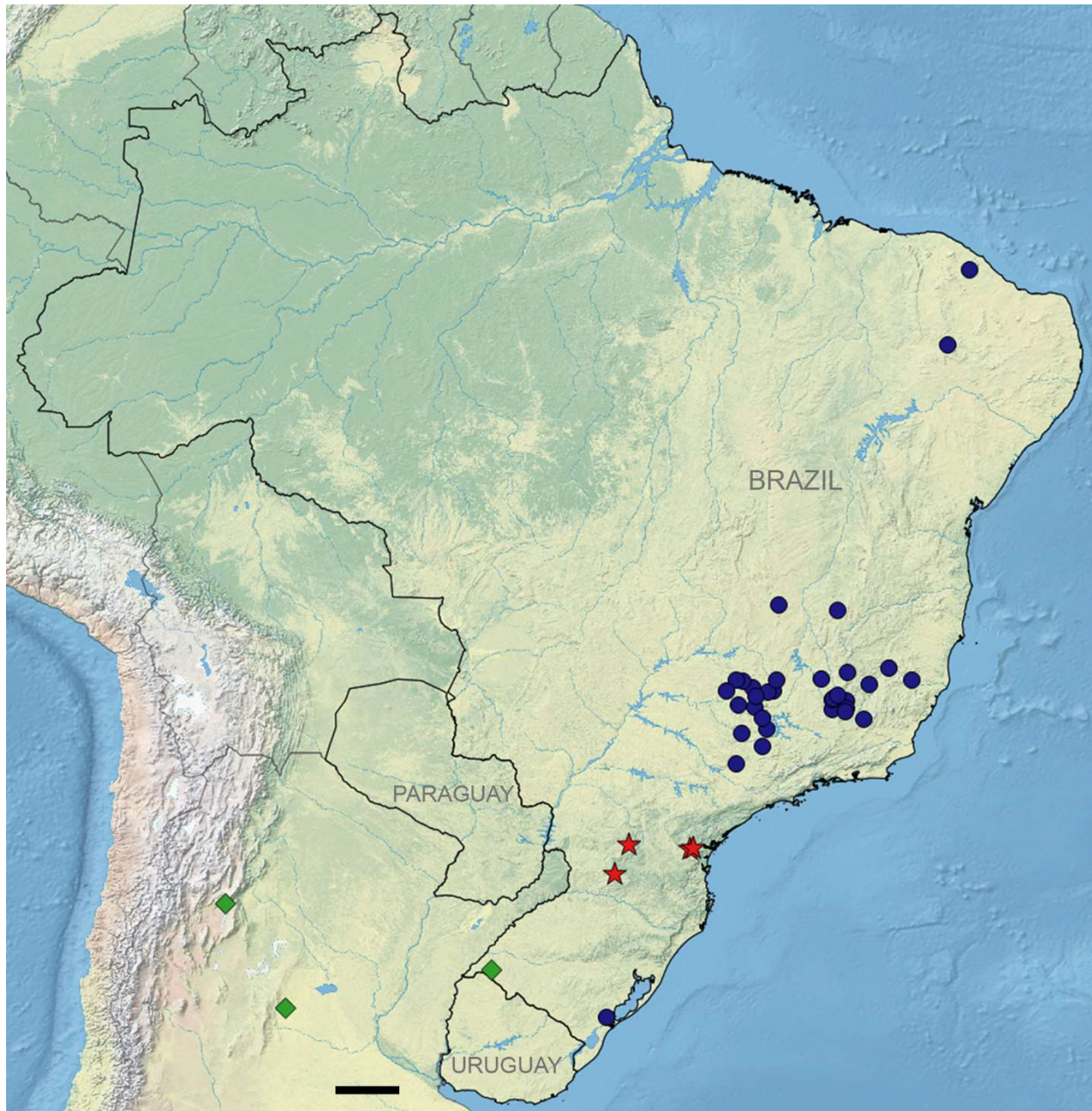
**Figure 18.** Dorsal view of the male terminalia of *Colletes furfuraceus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** ARGENTINA – Buenos Aires: Puan, Felipe Solá, i/1952, [Martinez], 1♂, {SEMC}; idem, except ii/1952, 10♂♂. Tandil, i/1952, 1♂, {SEMC}. Catamarca: Andalgalá, 18/x/1972, [J. Neff], 1♂, {SEMC}; idem, except 12/xi/1973, 2♂♂. Córdoba: Calera, xi/1952, [J. Foerster], 1♀, {SEMC}.

**Range:** ARGENTINA (Buenos Aires, Catamarca, Córdoba), Brazil (Rio Grande do Sul), PARAGUAY (Itapua, Misiones, Neembucu). See also Fig. 19.

**Biogeographical distribution:** Chacoan dominion (Chacoan and Pampean provinces), and South American transition zone (Monte province) at altitudes of 200–1200m a.s.l.

**DNA barcode:** Unavailable.



**Figure 19.** Geographical distribution of *Colletes furfuraceus* (green diamonds), *C. michenerianus* (red stars), and *C. rufipes* (blue circles). Scale bar approximately 250km.

**Floral hosts:** Capparaceae – *Atamisquea emarginata* Miers ex Hook. & Arn. (this study).  
 Compositae – *Baccharis* sp. (Jensen-Haarup 1908). Leguminosae – *Adesmia trijuga* Hook. &  
 Arn. (this study); *Prosopis nigra* Hieron. (this study). Loasaceae – *Blumenbachia insignis*  
 Schrad. (Schlindwein 1995, 1998). According to Jörgensen (1912a,b), *C. furfuraceus* also visits

the following plant species: Compositae – *Parthenium hysterophorus* L., *Senecio mendocinus* Phil. Leguminosae – *Geoffroea decorticans* (Hook. & Arn.) Burkart (as *Gourliea decorticans* Hook. & Arn.), *Prosopis alpataco* Phil. Malvaceae – *Sphaeralcea bonariensis* (Cav.) Griseb. Solanaceae – *Lycium chilense* Bertero. Tamaricaceae – *Tamarix Africana* Poir. Zygophyllaceae – *Larrea divaricata* Cav.

**Comments:** *Colletes furfuraceus* is a common species that is widely distributed in Argentina (from Catamarca in the northwest to Buenos Aires in the southeast) and also found in southern Brazil and Paraguay. According to the literature, the female visits flowers of at least ten plant families, which likely explains why the species is so widespread.

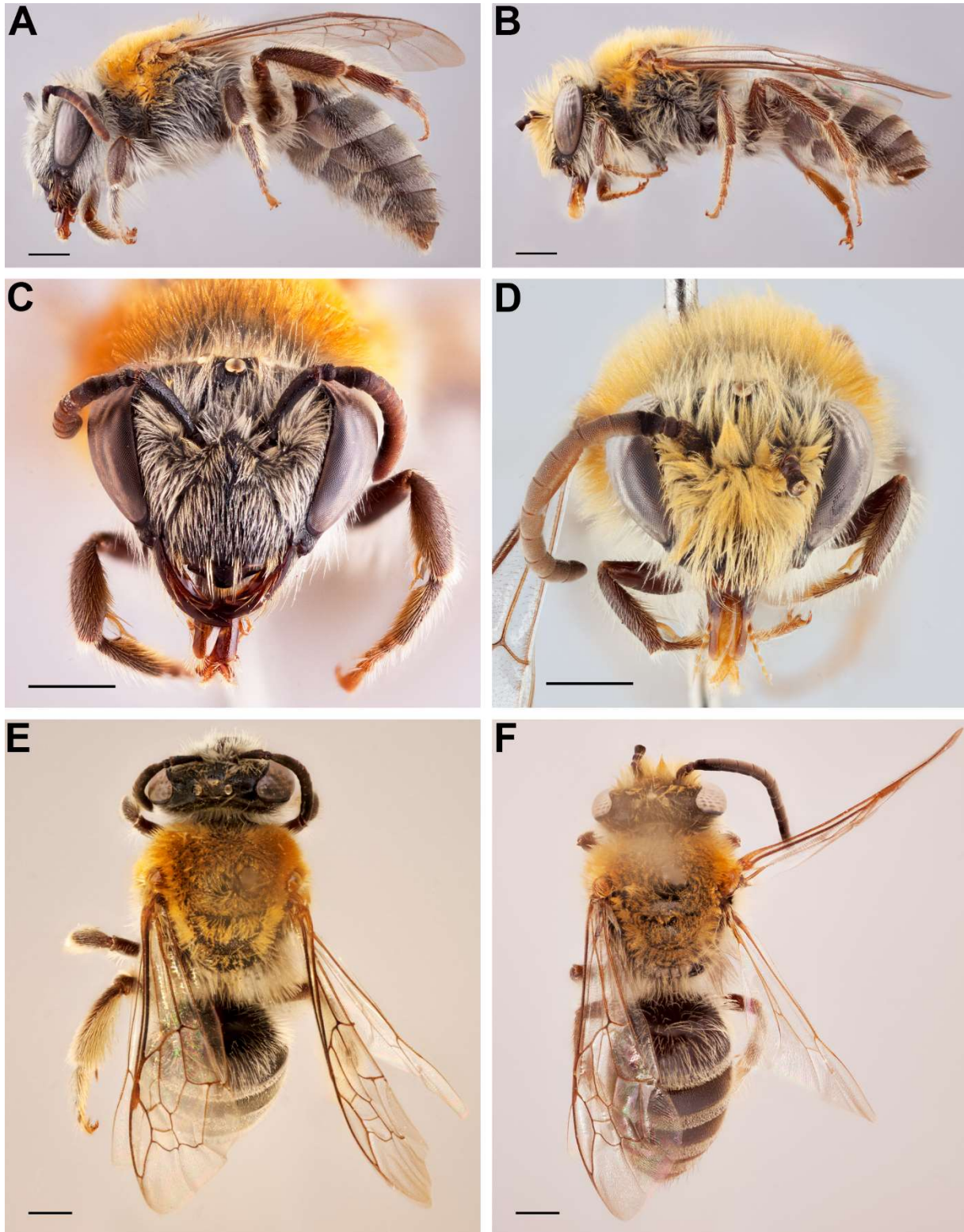
Regrettably, the female holotype of *C. furfuraceus* that was originally deposited at the MACN is lost (Roig-Alsina, *pers. comm.*). Nonetheless, its identity was established through examination of photographs of the female specimen that will be designated as the species' neotype in a different study (Roig-Alsina *et al.*, *in prep.*). The future neotype is also deposited at the MACN and is labelled as follows: “Neco;-chia”. “II. 18; 1920”. “Colletes; furfuraceus; Holmberg”. “Colletes ♀; furfuraceus Holmberg; NEOTYPUS; Ferrari, Compagnucci & Roig-Alsina”.

### ***Colletes hawkingi* Ferrari, new species**

(Figs. 20, 21, 22, 57A)

**Diagnosis:** Amongst the *Colletes* species found in Brazil, *C. hawkingi* **n. sp.** can be diagnosed through the combination of very short malar area,  $\sim 0.2/\sim 0.4 \times \text{MOD}$  (♀/♂), and legs with pale-yellow setae. The female of *C. hawkingi* **n. sp.** is most similar to that of *C. imbricatus* **n. sp.** (the male of the latter is unknown) as in both the mesosoma is covered with pale pubescence and the posterior hind tibial spur is pectinate. However, their females can be easily distinguished from each other by malar area  $\sim 0.2 \times$  as long as basal depth of mandible in *C. hawkingi* **n. sp.** (malar area subequal in length to depth of mandible in *C. imbricatus* **n. sp.**), and clypeus densely punctate with striate interspaces in *C. hawkingi* **n. sp.** (clypeus sparsely punctate with imbricate interspaces in *C. imbricatus* **n. sp.**).





**Figure 20.** *Colletes hawkingi* n. sp. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.



**Description:** FEMALE (Figs. 20A, 20C, 20E):

*Dimensions (mm):* Approximate body length 9.2; head width 3.0; head length 2.2; intertegular distance 2.5; forewing length 7.1.

*Colouration:* Black except mandible (except distal 1/3 marked on dark-yellow), labrum reddish-brown. Ventral surface of F3–F10 dark-orange. Tegula, tibial spurs, distal half of tarsal claws pale-orange. Legs (except dorsal surface of mediotarsi 3 and distitarsi pale-brown), ventrally reflexed lateral areas of T1–T4, discs of S2–S3, S6 posterolaterally dark-brown. Wing venation (except veins C and R of forewing dark-brown and black), stigma, proximal half of tarsal claws pale-brown. Tibial spurs, marginal zones of metasomal sterna pale-yellow.

*Structure:* Labrum medially concave; concavity not margined laterally by longitudinal ridges. Clypeal mid-longitudinal area not depressed. Malar area  $\sim 0.2x$  as long as basal depth of mandible (14:59). Hypostomal carina short and flat. F1 subequal in length to its apical width (28:29). UID:LID (57:51). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum pointed. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum  $\sim 0.6x$  as long as metanotum (28:46); metapostnotal pits well-delimited; posterior transverse carina straight and complete. Posteromedial surface of front coxa with weak spine. Posterior hind tibial spur pectinate. Hind basitarsus  $\sim 3.2x$  longer than broad (52:16). Outer rami of hind tarsal claws  $1.8x$  as long as inner rami (18:10). Marginal zone of T1 flat. Marginal zone of S6 depressed.

*Pubescence:* Head with pale-yellow, plumose, suberect, moderately long hairs; except mandible and clypeal subapical pits with setae; interantennal and upper paraocular areas with erect hairs; vertexal area (near occipital area) and genal area (towards proboscoidal area) with long hairs. Mesosoma with bright-orange, plumose, erect, moderately long hairs; except mesepisternum and metepisternum with off-white, long hairs; upper margin of lateral surface of propodeum with very long hairs. Legs with pale-yellow hairs (except femoral and tibial scopae with fuscous hairs); trochanters and femora with plumose, erect, long hairs; front and mid tibiae with suberect, short setae (except posterodorsal surface with erect, moderately short setae); hind tibia and basitarsi with erect, moderately long setae (except posterior margin of mid basitarsus and hind tibia and basitarsus with long setae). T1 disc with pale-yellow, plumose, erect, long hairs; T2–T5 discs with pale-yellow, suberect, minute setae (T4–T5 also with fuscous, erect,

long setae); T1–T5 marginal zones covered with off-white, plumose, appressed, short hairs; T6 with pale-yellow, suberect, moderately short setae throughout. Metasomal sterna with pale-yellow hairs throughout; S1 with plumose, erect, moderately long hairs; S1 discs with plumose, erect, moderately long hairs; S2–S5 discs with erect, moderately short setae (such setae minute anteriorly and mid-longitudinally); S1–S5 marginal zones with a line of plumose, suberect, moderately long hairs; S6 with moderately short setae throughout, these setae suberect anteriorly, erect towards posterior margin.

*Surface sculpture:* Clypeus moderately coarsely punctate; punctures ill-defined and coalescent; interspaces striate. Supraclypeal area sparsely and moderately coarsely punctate on disc; lateral slopes densely punctate; interspaces rugulose throughout. Malar area substrigulate. Paraocular area densely and moderately finely punctate (except slightly coarser towards antennal socket); punctures below ill-defined; interspaces rugulose. Frontal area densely and moderately coarsely punctate; interspaces rugulose. Vertexal area densely and finely punctate near lateral ocellus; minutely punctate elsewhere; interspaces smooth throughout. Mesoscutum and scutellum densely and coarsely punctate (except mesoscutum moderately coarsely punctate anterolaterally and sparsely punctate posteromedially, and scutellum with punctures crowded and moderately fine posteriorly); interspaces smooth. Metanotum punctures crowded and moderately coarse; interspaces rugose. Mesepisternum densely and coarsely punctate (except punctures finer towards ventral surface and posteriorly); interspaces smooth. Metepisternum with oblique carinae mid-anteriorly; rugose above, densely and moderately coarsely punctate below. Lateral surface of propodeum moderately finely punctate; sparsely punctate below; densely punctate above; interspaces smooth. Vertical surface of metapostnotum with transverse carina above. Metasomal terga with smooth interspaces throughout; T1–T4 minutely punctate, T1 sparsely punctate, T2–T4 moderately densely punctate; T5 densely and finely punctate; T6 punctures crowded and moderately fine. Metasomal sterna with imbricate interspaces throughout; S2–S5 moderately densely and finely punctate (except S5 densely punctate); S6 densely and moderately finely punctate, punctures limits difficult to tell apart.

MALE (Figs. 20B, 20D, 20F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 8.4; head width 2.7; head length 2.0; intertegular distance 2.2; forewing length 6.4.

*Colouration*: Mandible medially dark-orange. Ventral surface of F2–F11, mid basitarsus and mediotarsi 1–2, discs of S2–S3, S6 pale-brown. Discs of T3–T6 dark-brown.

*Structure*: Malar area  $\sim 0.4x$  as long as basal depth of mandible (24:53). F1  $0.8x$  as long as its apical width (25:33). UID:LID (56:45). Dorsolateral angle of pronotum modified as a long spine. Horizontal surface of metapostnotum  $\sim 0.7x$  as long as metanotum (31:46); posterior transverse carina somewhat sinuous. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 3.4x$  longer than broad (5:16). Outer rami of hind tarsal claws  $\sim 1.2x$  as long as inner rami (10:8). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 21A, 21B, 21C, respectively.

*Pubescence*: Head with bright-yellow pubescence; clypeal subapical pits with plumose hairs; facial hairs longer than those on vertexal area. Mesosoma dorsally covered with bright-yellow, long hairs; mesepisternum and metepisternum with pale-yellow hairs. Metasomal terga with pale-yellow appressed hairs on marginal zones. S2 disc with plumose hairs. S2–S5 with broader bands of appressed hairs medially. S6 with suberect setae throughout.

*Surface sculpture*: Clypeus densely and moderately finely punctate; punctures well-delimited above, coalescent below. Supraclypeal area punctures crowded and fine; interspaces rugose. Mesepisternum moderately sparsely punctate towards ventral surface. Vertical surface of metapostnotum with transverse carina above. T1–T3 moderately finely punctate. T3–T4 finely punctate. T4–T5 with imbricate interspaces. S6 finely punctate.

**Type material**: *Holotype* ♀ – “CHÃ GRANDE, PE; Brasil, 4.11.2001; Milet & Pinto da Silva”. “L127 coletado no; vidro 13:00”. “7315 UFPE”. “Colletes sp. (PE atual); A 1137; Schlindwein det. 2003”. “CCDB-30344 G5”. “HOLOTYPE; Colletes hawkingi ♀; Ferrari, new species”. {UFMG}.

*Paratypes*: **BRAZIL – Ceará**: Santana do Cariri, Chapada do Araripe, 8/ii/2001, [A. Carvalho], 1♀, {UFMG}. **Pernambuco**: Chã Grande, 30/ix/2001, [Milet & Morais], 1♂, {UFMG}.

**Range:** BRAZIL (Ceará, Pernambuco). See also Fig. 22.

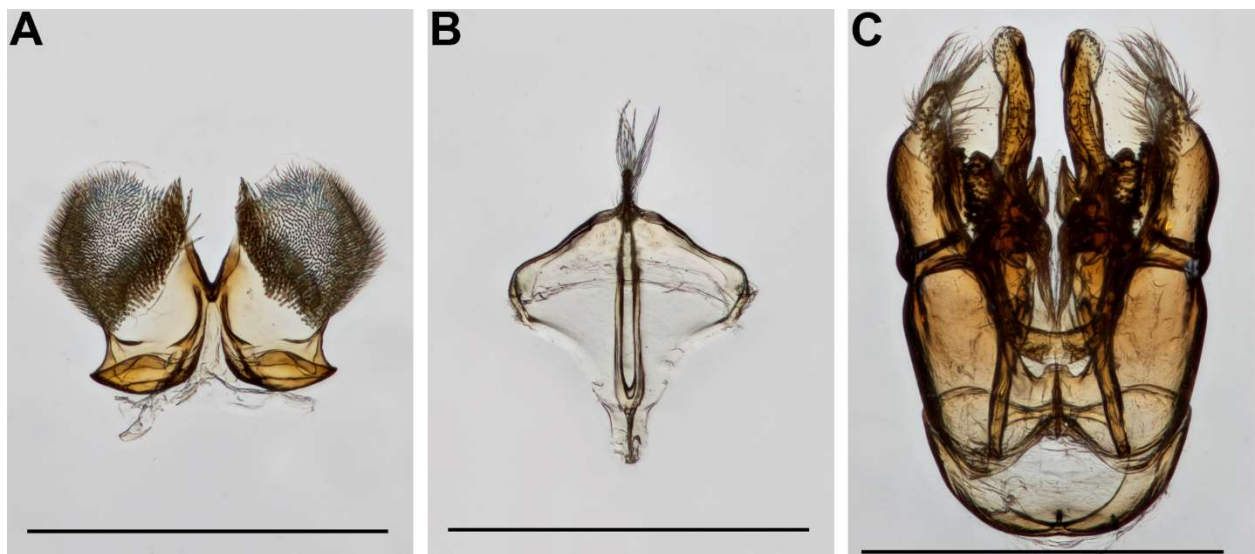
**Biogeographical distribution:** Chacoan dominion (Caatinga province), and Parana dominion (Atlantic province) at altitudes of 400–800m a.s.l.

**DNA barcode:** A non-BIN-compliant sequence (422 bp) is available for one female specimen (CCDB-30383-D05).

**Floral hosts:** Unknown.

**Etymology:** Species named after the astrophysicist Stephen W. Hawking (1942–2018), one of the most brilliant minds of all times.

**Comments:** Rare species that appears to be endemic to northeastern Brazil, although it is known from two different ecoregions there—the Atlantic rainforest and the Caatinga.



**Figure 21.** Dorsal view of the male terminalia of *Colletes hawkingi* n. sp. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

***Colletes imbricatus* Ferrari, new species**

(Figs. 23, 24)

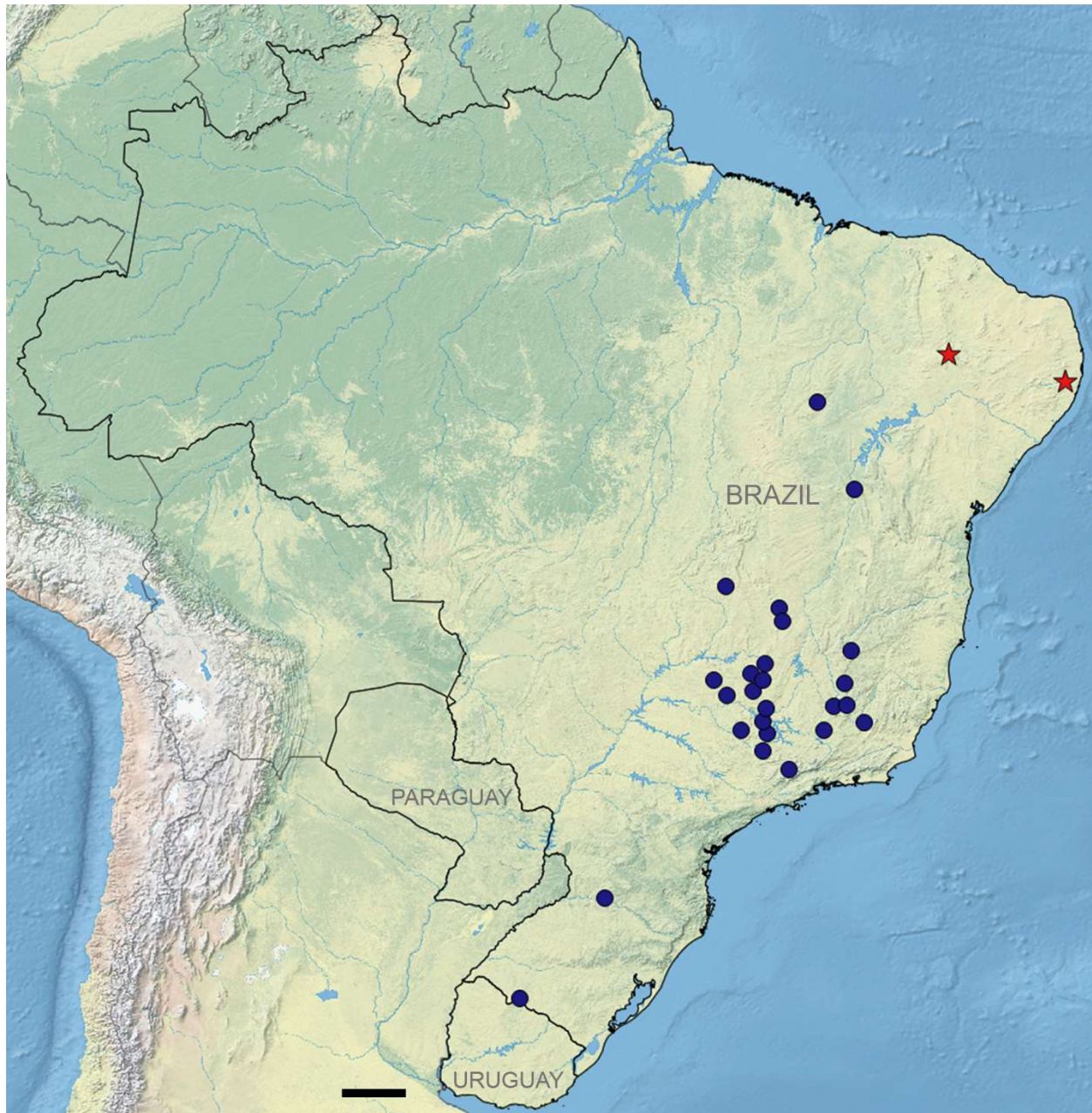
**Diagnosis:** The combination of mesepisternum with imbricate insterspaces, and T2–T5 entirely covered with pale-yellow hairs is sufficient to distinguish *C. imbricatus* **n. sp.** from all other species of the genus found in Brazil. *Colletes imbricatus* **n. sp.** is most similar to *C. hawkingi* **n. sp.** as in both the mesosoma is covered with pale pubescence and the posterior hind tibial spur is pectinate. However, the females of the two species (the male of *C. imbricatus* **n. sp.** is unknown) can be differentiated from each other by malar area subequal in length to depth of mandible in *C. imbricatus* **n. sp.** (malar area  $\sim 0.2\times$  as long as basal depth of mandible in *C. hawkingi* **n. sp.**), and clypeus sparsely punctate with imbricate interspaces in *C. imbricatus* **n. sp.** (clypeus densely punctate with striate interspaces in *C. hawkingi* **n. sp.**).

**Description:** FEMALE (Figs. 23A–C):

*Dimensions (mm):* Approximate body length 9.9; head width 3.4; head length 2.7; intertegular distance 2.9; forewing length 7.8.

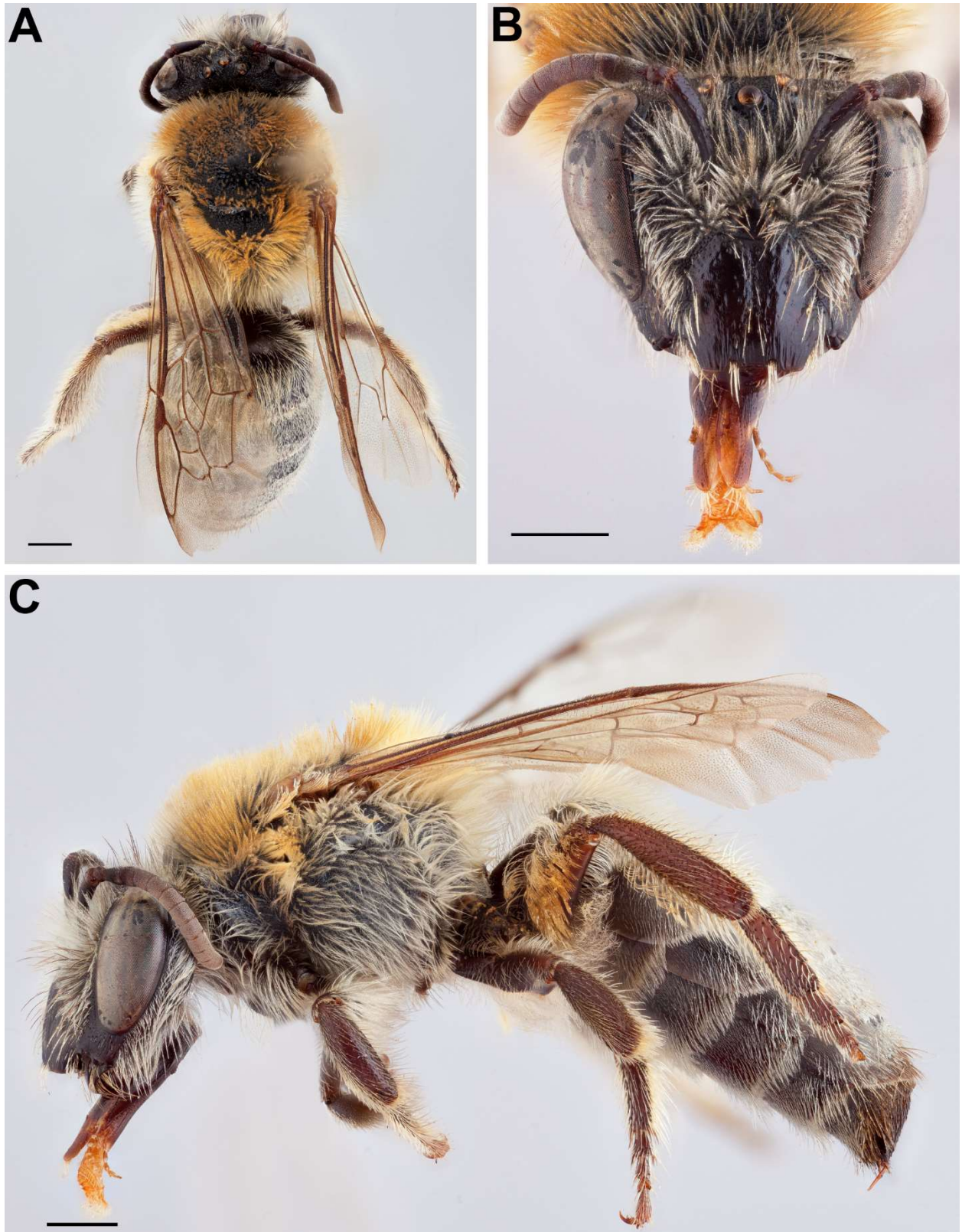
*Colouration:* Black except distal half of mandible, malar area below, clypeus laterally reddish-brown. Ventral surface of F2–F10, stigma, legs (except dorsal surface of distitarsi and hind tibia and basitarsus pale-brown), ventrally inflexed lateral area of T1–T3, marginal zones of T4–T5 dark-brown. Tegula, wing venation (except forewing veins R black and C dark-brown), tibial spurs, distal 2/3 of tarsal claws dark-orange. Marginal zones of T1–T3 pale-brown. Proximal 1/3 of tarsal claws, marginal zones of metasomal sterna pale-yellow.

*Structure:* Labrum medially concave; concavity margined laterally by longitudinal ridges. Clypeal mid-longitudinal area shallowly depressed throughout; depression relatively narrow ( $0.6\times$  MOD) above, broader ( $0.9\times$  MOD) below. Malar area subequal in length to basal depth of mandible (41:43). Hypostomal carina short and flat. F1  $\sim 1.2\times$  as long as its apical width (30:24). UID:LID (67:63). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum triangular acute. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by short hairs. Horizontal surface of metapostnotum  $\sim 0.4\times$  as long as metanotum (20:48); metapostnotal pits well-delimited; posterior transverse carina straight and incomplete.



**Figure 22.** Geographical range of *Colletes hawkingi* n. sp. (red stars), and *C. meridionalis* (blue circles). Scale bar approximately 250km.





**Figure 23.** *Colletes imbricatus* n. sp. Female: (A) habitus, dorsal view (B); face, frontal view; (C) habitus, lateral view. Scale bars = 1mm.

Posteromedial surface of front coxa without spine. Posterior hind tibial spur pectinate. Hind basitarsus ~3.2x longer than broad (52:16). Outer rami of hind tarsal claws ~2x as long as inner rami (15:7). Marginal zone of T1 flat. Marginal zone of S6 depressed.

*Pubescence:* Head with pale-yellow, plumose, erect, moderately long hairs; except mandible and clypeal subapical pit with setae; paraocular area with pale-yellow and black hairs intermixed; genal area with appressed hairs above; vertexal area with black long hairs near occipital area. Mesosoma with pale-orange, plumose, erect, long hairs; except mesepisternum, metepisternum and upper margin of lateral surface of propodeum with pale-yellow, very long hairs; disc of lateral surface of propodeum with appressed, moderately short hairs. Legs with pale-yellow, erect, moderately long setae; except anteroventral surface of trochanters and ventral surface of femora with plumose, long hairs; femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; front and mid tibiae with suberect, moderately short setae anterodorsally; basitarsi with long setae on posterior margin (hind basitarsus with very long setae). Mesosomal terga covered with pale-yellow, plumose, appressed, short hairs (except T6 with fuscous, suberect, moderately short setae); T1 also with erect, very long hairs; T2–T3 with erect, moderately short hairs laterally; T4 with erect, moderately long setae; those setae fuscous and long on T5. Metasomal sterna with pale-yellow hairs (except S6 with fuscous hairs near posterior margin); S1 with plumose, erect, moderately long hairs; S2 disc with branched apically only, erect, moderately short hairs; S3–S6 discs with suberect, short setae (except S5 posteriorly and S6 with moderately long setae); S2–S5 marginal zones with a transverse line of plumose, suberect, moderately short hairs.

*Surface sculpture:* Clypeal mid-longitudinal depression moderately densely and moderately finely punctate; adjacent convex area sparsely punctate; lower area longitudinally striate; interspaces imbricate throughout. Supraclypeal area imbricate. Malar area moderately densely and finely punctate above (interspaces imbricate); substrigulate below. Paraocular area densely and moderately finely punctate (except moderately densely punctate towards antennal socket and above); interspaces imbricate. Frontal area punctures difficult to discern from coarsely imbricate interspaces. Vertexal area densely punctate; moderately fine and minute punctures intermingled; interspaces smooth (except rugose near lateral ocellus). Mesosoma with imbricate interspaces throughout. Mesoscutum densely and moderately coarsely punctate (except punctures sparse and coarse posteromedially). Scutellum densely and moderately coarsely

punctate anteriorly; punctures crowded and moderately fine posteriorly. Metanotum punctures crowded and moderately fine. Mesepisternum densely and coarsely punctate (except punctures sparser towards ventral surface). Metepisternum with oblique carinae mid-anteriorly; densely and moderately coarsely punctate above and below. Lateral surface of propodeum densely and finely punctate. Vertical surface of metapostnotum rugose above. Metasomal terga sparsely and minutely punctate throughout; interspaces smooth. Metasoma sterna with imbricate interspaces; S1 sparsely and finely punctate; S2–S4 moderately sparsely and moderately finely punctate (except densely and finely punctate laterally and near marginal zones); S5 densely and finely punctate; S6 densely and finely punctate anteriorly; sparsely and moderately finely punctate posteriorly.

MALE: Unknown.

**Type material:** *Holotype* ♀ – “CAÇAPAVA RS; Min. do Camaquã; Brasil 10.11 1990; C. Schlindwein leg.”. “PUC/RS – Univ. Tübingen; Lab. Pesq. Biológicas; 1957-313; F.40 17h”. “*Colletes* sp 2; ♀”. “CCDC-30383 C12”. “HOLOTYPE; *Colletes imbricatus* ♀; Ferrari, new species”. {UFMG}.

*Paratypes:* **BRAZIL – Rio Grande do Sul:** Caçapava do Sul, Minas de Camaquã, 25/x/2009, [C. Schlindwein], 2♀♀, {UFMG}.

**Range:** BRAZIL (Rio Grande do Sul). See also Fig. 24.

**Biogeographical distribution:** Chacoan dominion (Pampean province) at altitudes of 300–600m a.s.l.

**DNA barcode:** Unavailable.

**Floral hosts:** Loasaceae – *Blumenbachia insignis* Schrad.

**Etymology:** Reference to the fact that its mesosoma has imbricate interspaces, an uncommon feature amongst the *Colletes* species found in Brazil.





**Figure 24.** Geographical range of *Colletes imbricatus* **n. sp.** (red star), and *C. rugicollis* (blue circles). Scale bar approximately 250km.

**Comments:** Seemingly a rare species that appears to be associated with the South American Pampas ecoregion.

***Colletes kerri* Moure, 1956**

(Figs. 4, 25, 26, 56A)

*Colletes kerri* Moure, 1956: 197; Michener & Lange 1957: 79; Michener *et al.* 1958a: 10, 1958b: 208; Rozen 1966: 12, 1991: 29; Roig-Alsina 1991: 259; Moure & Urban 2002: 11; Silveira *et al.* 2002: 155; Moure *et al.* 2007: 683; Moure *et al.* 2012; Ramos *et al.* 2015: 338; Ascher & Pickering 2018.

Holotype ♀ examined. (DZUP).

**Diagnosis:** *Colletes kerri* is diagnosable by having clypeus and supraclypeal area longitudinally finely striate. This species is most similar to *C. ferenudus* **n. sp.** as in their females (the male of the latter is unknown) the mesoscutal pubescence is pale-orange, and T2–T5 are covered with sparse short setae, without dense appressed hairs. The females of the two species, however, can be distinguished from one another by labrum convex medially in *C. kerri* (labrum concave medially in *C. ferenudus* **n. sp.**); and mesepisternum with smooth interspaces in *C. kerri* (mesepisternum with imbricate interspaces in *C. ferenudus* **n. sp.**).

**Redescription:** FEMALE (Figs. 25A, 25C, 25E):

*Dimensions (mm):* Approximate body length 11.4–11.9; head width 3.6–3.8; head length 3.0–3.2; intertegular distance 3.2–3.5; forewing length 8.7–9.0.

*Colouration:* Black except distal 2/3 of mandible (apical tooth with dark-yellow spot distally), distal half of tarsal claws reddish-brown. Ventral surface of F3–F10 (except F10 pale-brown apically), wing venation (except vein R of forewing black), stigma, anteroventral surface of femora, dorsal surface of tibiae and tarsi (except distitarsi pale-brown), proximal half of tibial spurs, marginal zones of T1–T5, ventrally reflexed lateral area of T1, S2–S5 posteromedially, S6 anteriorly and laterally dark-brown. Distal half of tibial spurs, proximal half of tarsal claws, ventrally inflexed lateral area of T6, S6 mid-longitudinally pale-brown. Tegula pale-orange. T1–T5 discs with blueish reflections. Marginal zones of S1–S5 pale-yellow.





**Figure 25.** *Colletes kerri* Moure, 1956. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.



*Structure:* Labrum medially convex; concavity not margined laterally by longitudinal ridges. Clypeal mid-longitudinal area evenly broadly (1.4x MOD) depressed throughout; depression shallow above, somewhat deeper below. Malar area ~0.9x as long as basal depth of mandible (41:46). Hypostomal carina short and flat. F1 ~1.5x as long as its apical width (44:30). UID:LID (72:68). Frontal area without protrusion below lateral ocellus. Vertexal area flat behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum rounded. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum ~0.3x as long as metanotum (17:66); metapostnotal pits well-delimited; posterior transverse straight and incomplete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.5x longer than broad (60:17). Outer rami of hind tarsal claws ~2.3x as long as inner rami (16:7). Marginal zone of T1 flat. Marginal zone of S6 depressed.

*Pubescence:* Head with off-white, plumose, erect, moderately long hairs; except mandible and clypeal subapical pit with fuscous setae; paraocular, frontal and vertexal areas with off-white and black hairs intermixed; genal area (towards proboscidal area) and vertexal area (near occipital area) with long hairs. Mesosoma with pale-orange, plumose, erect, long hairs; except pronotal and mesoscutal hairs somewhat shorter than those of scutellum; mesepisternum and metepisternum with pale-yellow very long hairs; lateral surface of propodeum with appressed, moderately short hairs on disc. Legs with fuscous, erect, moderately long setae; except trochanters and femora with pale-yellow, plumose, erect, long hairs anteroventrally; femoral and tibial scopae with pale-yellow, branched apically only, suberect, very long hairs anteriorly; dorsal surface of front and mid tibiae with suberect, short setae; basitarsi with very long setae on posterior margins. Metasomal terga with fuscous, suberect, minute setae on discs; except T1 with pale-yellow, plumose, erect, long hairs (those hairs suberect and moderately short laterally); T4–T5 with erect, moderately long setae (those setae long laterally); T6 entirely covered with black, suberect, moderately long setae; T1 marginal zone with off-white, plumose, appressed, short hairs; T2–T3 with distal bands of appressed hairs largely interrupted medially. Metasomal sterna pale-yellow, erect, moderately short setae; except S1 with plumose, long hairs; S2 with branched apically only, moderately long hairs; S2–S3 with a transverse line of branched apically only, suberect, short hairs near marginal zones; S4–S5 with long setae near marginal zones; S6 with fuscous setae posterolaterally.

*Surface sculpture:* Clypeal mid-longitudinal depression impunctate and smooth; convex area substrigulate near depression, sparsely and moderately finely punctate towards lateral slopes (interspaces smooth). Supraclypeal area substrigulate. Malar area sparsely and moderately finely punctate; interspaces substrigulate. Paraocular area densely and moderately coarsely punctate (except punctures somewhat sparser towards antennal socket and finer near lower end of facial fovea); interspaces smooth throughout. Frontal area densely and coarsely punctate; interspaces rugulose. Vertexal area sparsely and minutely punctate (except densely and moderately finely punctate posteriorly); interspaces smooth. Mesoscutum densely and coarsely punctate; interspaces smooth. Scutellum and metanotum with punctures crowded and moderately coarse (except scutellum coarsely punctate anteriorly); interspaces rugose. Mesepisternum punctures crowded and coarse anterior to episternal groove and below scrobe; punctures somewhat sparser ventrally; interspaces smooth. Metepisternum with oblique carinae mid-anteriorly; punctures crowded and moderately coarse above and below (interspaces rugose). Lateral surface of propodeum sparsely and finely punctate; punctures difficult to discern from overall rugulose interspaces. Vertical surface of metapostnotum rugose above. Metasomal terga sparsely and minutely punctate (except T6 moderately sparsely and finely punctate); T1–T5 with minute and moderately fine punctures intermingled (more markedly on T5); interspaces smooth (except imbricate on T5–T6). S1–S2 sparsely and finely punctate; S3–S5 densely and finely punctate (except punctures somewhat coarser laterally); S6 densely and moderately coarsely punctate (except minutely punctate anteriorly and mid-longitudinally); interspaces imbricate on S1, S5 and S6, smooth on S2–S4.

MALE (Figs. 25B, 25D, 25F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 10.0–10.4; head width 3.2–3.5; head length 2.7–2.9; intertegular distance 3.1–3.3; forewing length 8.0–8.4.

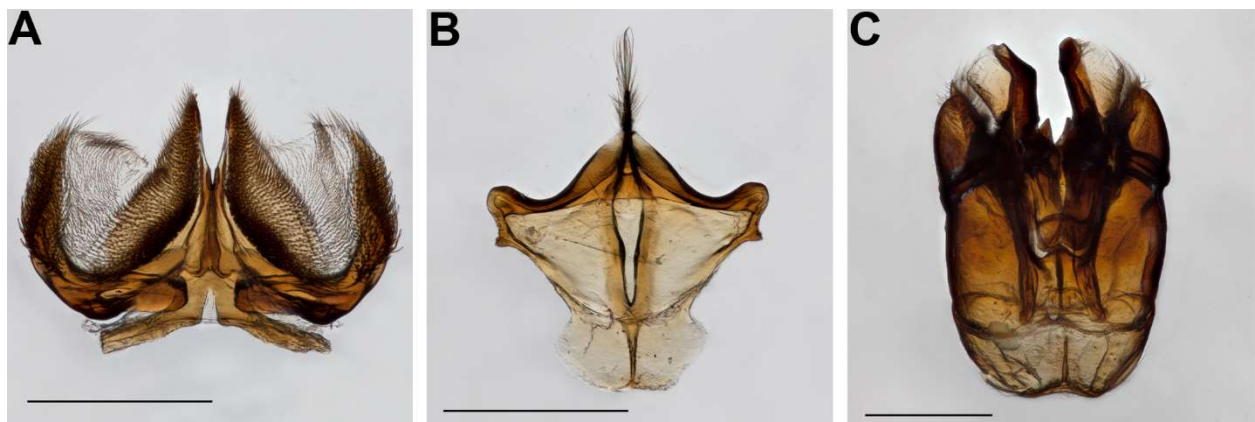
*Colouration:* Mandibular apical tooth entirely reddish-brown. Ventral surface of F2 dark-brown. Veins M+Cu and V of forewing pale-brown. Legs dark-brown (except trochanters black and dorsal surface of front and mid distitarsi and hind tarsus pale-brown). S6 disc dark-brown.

*Structure:* Labrum medially flat. Clypeal mid-longitudinal area deeply depressed; depression relatively narrow (0.8x MOD) above, much broader (maximum width 2.4x MOD)

below. Malar area 0.8x as long as basal depth of mandible (36:45). F1 subequal in length to its apical width (27:26). UID:LID (67:59). Vertexal area concave behind upper summit of eye in postero-lateral view. Horizontal surface of metapostnotum  $\sim 0.3$ x as long as metanotum (19:72); metapostnotal pits poorly-delimited; posterior transverse sinuous. Hind basitarsus  $\sim 3$ x longer than broad (53:18). Outer rami of hind tarsal claws  $\sim 1.9$ x as long as inner rami (15:8). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 26A, 26B, 26C, respectively.

*Pubescence*: Frontal area with black hairs only. Pronotal and mesoscutal hairs as long as those of scutellum. Lateral surface of propodeum with erect hairs throughout. Legs with pale-yellow setae (except tibiae with fuscous setae posteriorly). Mid and hind basitarsi with long setae on dorsal surface. T2 disc with pale-yellow, plumose, erect, moderately short hairs. S2 with plumose hairs. S6 with suberect setae (except setae erect posterolaterally).

*Surface sculpture*: Clypeal mid-longitudinal depression sparsely and moderately finely punctate; convex area smooth throughout (except substrigulate below). Supraclypeal area substrigulate mid-longitudinally, smooth laterally. Paraocular area punctures crowded above. Lateral surface of propodeum with well-delimited, moderately coarse punctures; interspaces imbricate. T1 densely and moderately finely punctate. T2–T3 moderately densely and finely punctate. T2–T4 with imbricate interspaces. T6 sparsely and minutely punctate. S2–S5 minutely punctate mid-longitudinally. S6 sparsely and minutely punctate (except densely and moderately finely punctate anterolaterally). S2–S6 with smooth interspaces posteriorly.



**Figure 26.** Dorsal view of the male terminalia of *Colletes kerri*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** *Primary type specimen:* Holotype ♀ – “HOLOTIPO”. “Araucaria; 28-i-56; PARANÁ”. “KERRI”. {DZUP}.

*Secondary type specimens:* Paratypes ♀♀ and ♂♂ – **BRAZIL – Paraná:** Araucária, 28/i/1956, [W. Kerr], 4♀♀4♂♂, {DZUP}; idem, except 2♀♀1♂, {SEMC}.

*Additional specimens:* **BRAZIL – Paraná:** Campina Grande do Sul, 17/ii/2007, [Melo & Vivallo], 1♀, {DZUP}.

**Range:** BRAZIL (Paraná). See also Fig. 4.

**Biogeographical distribution:** Parana dominion (*Araucaria* forest province) at altitudes of 800–100m a.s.l.

**DNA barcode:** Unavailable.

**Floral hosts:** Unknown

**Comments:** Uncommon species likely endemic to the *Araucaria* forest ecoregion in southern Brazil.

Individuals of the cuckoo *Isepeolus viperinus* (Holmberg, 1886) (Hymenoptera: Apidae) were found in the nests of *C. kerri* from which the type specimens of the host were obtained by W. Kerr (Moure 1956).

### ***Colletes meridionalis* Schrottky, 1902**

(Figs. 22, 27, 28, 52A, 55C, 56B, 57B)

*Colletes rufipes meridionalis* Schrottky, 1902: 345; Schrottky 1913: 236; Cruz-Landim 1968: 119, 1973: 209; Rasmussen *et al.* 2009: 31; Ramos *et al.* 2015: 349.

Lectotype ♀ examined. Designated by Ferrari & Silveira (2015: 260). (MZSP).

*Colletes extensicornis* Vachal, 1909: 53; Moure & Urban 2002: 9; Silveira *et al.* 2002: 155; Moure *et al.* 2007: 681; Azevedo *et al.* 2008: 150; Carvalho & Oliveira 2010: 48; Moure *et al.*

2012; Rasmussen 2012: 27; Lima & Silvestre 2017: 11. Synonymy proposed by Ferrari & Silveira (2015: 260).

Lectotype ♂ examined. Designated by Moure & Urban (2002: 9). (MNHP).

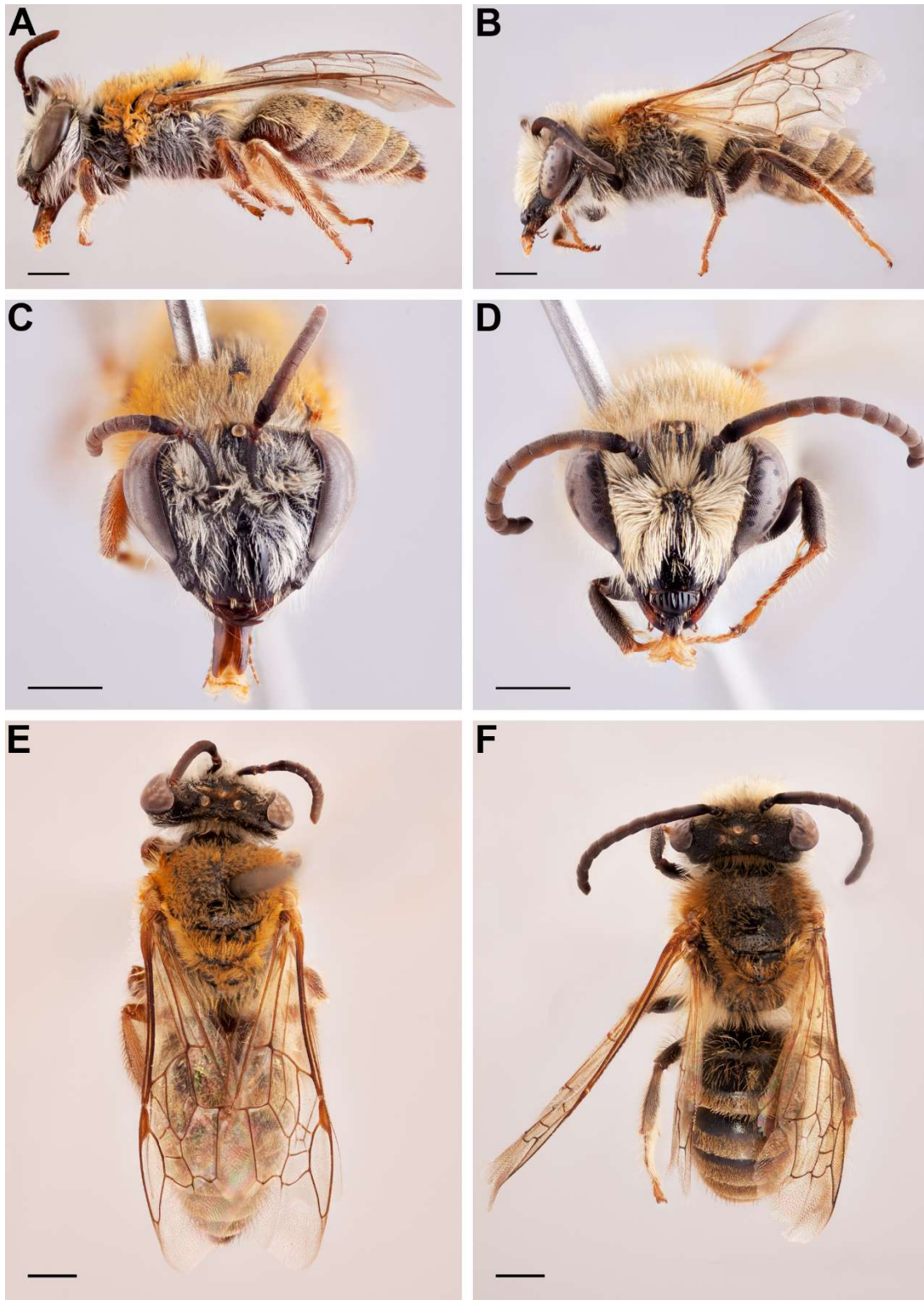
*Colletes meridionalis*; Moure 1945: 394; Moure & Urban 2002: 13; Silveira *et al.* 2002: 155; Moure *et al.* 2007: 683; Azevedo *et al.* 2008: 150; Moure *et al.* 2012; Ferrari & Silveira 2015: 260; Ascher & Pickering 2018.

**Diagnosis:** *Colletes meridionalis* is unique in having the ventral surface of mesepisternum with a protrusion near the end of episternal groove that is surrounded by appressed short hairs. The only other *Colletes* species known to me that also has this characteristic is *C. brevinodis* Vachal, 1909 from Bolivia which most likely is the sister-species of *C. meridionalis*. However, the males of the two species (the female of *C. brevinodis* remains unknown) can be differentiated from one another by femora and tibiae dark-brown to black in *C. meridionalis* (femora and tibiae pale-yellow in *C. brevinodis*); and mesepisternum densely punctate in *C. meridionalis* (mesepisternum sparsely punctate in *C. brevinodis*). In Brazil, *C. meridionalis* is most similar to *C. pampeanus* n. sp. because both are virtually the same size (10/8mm in length (♀/♂)), and their legs are essentially covered with pale-yellow setae and metasomal terga with pale-yellow appressed hairs. However, these species can be distinguished from each other by the unique feature of *C. meridionalis* mentioned above; and malar area considerably shorter, ~0.6/~1.3x (♀/♂) as long as basal depth of mandible, in *C. meridionalis* (malar area ~1.2/2.0x (♀/♂) as long as basal depth of mandible in *C. pampeanus* n. sp.).

**Redescription:** FEMALE (Figs. 27A, 27C, 27E):

*Dimensions (mm):* Approximate body length 9.2–10.2; head width 3.3–3.6; head length 2.4–2.6; intertegular distance 2.5–2.8; forewing length 7.4–7.9.

*Colouration:* Black except distal half of mandible and tarsal claws reddish-brown. Femora (except distal ring of hind femur pale-brown), front and mid tibiae, ventrally reflexed lateral areas of T1–T5, metasomal sterna (except S6 pale-brown mid-longitudinally) dark-brown. Vein R of forewing, front and mid tarsi, hind tibia (except proximal 1/5 of dorsal surface dark-brown) pale-brown.



**Figure 27.** *Colletes meridionalis* Schrottky, 1902. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.



Tegula, vein C of forewing, hind tarsus, proximal half of tarsal claws dark-orange. Wing venation (except veins C and R of forewing), tibial spurs, marginal zones T1–T5 and sterna pale-yellow.

*Structure:* Labrum medially concave; concavity margined laterally by longitudinal ridges. Clypeal mid-longitudinal area very narrowly (0.4x MOD) and moderately deeply depressed. Malar area ~0.6x as long as basal depth of mandible (32:55). Hypostomal carina short and flat. F1 ~1.1x as long as its apical width (29:27). UID:LID (66:63). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum modified as a long spine. Mesepisternum ventrally, near ventral end of episternal groove, with protrusion surrounded by short hairs. Horizontal surface of metapostnotum ~0.5x as long as metanotum (21:44); metapostnotal pits well-delimited; posterior transverse carina somewhat sinuous and complete. Posteromedial surface of front coxa with strong spine. Posterior hind tibial spur ciliate. Hind basitarsus ~4.3x longer than broad (52:12). Outer rami of hind tarsal claws ~2x as long as inner rami (17:8). Marginal zone of T1 flat. Marginal zone of S6 depressed.

*Pubescence:* Head with pale-yellow, plumose, erect, moderately long hairs, (except mandible with pale-orange setae); those hairs short on clypeal disc, long near occipital area; genal area with off-white, suberect, short hairs near outer margin of eye pubescence. Mesosoma covered with pale-orange, plumose, erect, long hairs; those hairs only moderately long on mesoscutum and scutellum, very long on upper margin of lateral surface of propodeum; mesepisternum and metepisternum with off-white hairs; lateral surface of propodeum with off-white, short, appressed hairs. Legs with pale-yellow hairs; trochanters and femora with plumose, erect, very long hairs (except hind trochanter with very long hairs); femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; tibiae with short setae, suberect on dorsal surface, erect on posterior surface (except hind tibia with erect, moderately short setae on dorsal and posterior surfaces); basitarsi with suberect, short setae on dorsal surface, those setae erect, long on posterior margin (except hind basitarsus with very long setae on dorsal margin). Metasomal terga covered with bright-yellow, dense, appressed hairs (except T6 with black, suberect, short setae); T1 also with plumose, erect, long hairs; T3–T5 also with erect, short setae on discs (those setae longer laterally). Metasomal sterna with pale-yellow hairs; T1 with plumose, erect, long hairs; T2–T6 with erect, minute setae on discs (T2 also with hairs branched

only apically); T2–T6 with plumose, suberect, short hairs on marginal zones (except T5 with moderately short setae).

*Surface sculpture:* Clypeus moderately densely and moderately coarsely punctate near mid-longitudinal depression; lateral slopes densely and moderately finely punctate towards paraocular area; coarsely striate towards lower margin; interspaces smooth throughout. Supraclypeal area sparsely and moderately coarsely punctate; interspaces imbricate. Malar area moderately sparsely and moderately finely punctate; interspaces finely striate. Paraocular area densely punctate throughout (except slightly sparser towards antennal socket); moderately coarsely punctate below (interspaces smooth); finer above (interspaces rugulose). Frontal area punctures crowded and coarse; interspaces rugulose. Vertexal area moderately sparsely and finely punctate near eye; punctures crowded and moderately fine near lateral ocellus; interspaces smooth (except small impunctate area near ocellus with rugulose integument). Mesoscutum and mesepisternum densely and coarsely punctate (except punctures sparse posteromedially); interspaces smooth throughout. Scutellum punctures crowded and moderately coarse (except punctures dense and coarse anteriorly); interspaces rugulose (except interspaces smooth anteriorly). Metanotum densely and moderately coarsely punctate; interspaces rugulose. Metepisternum with oblique carinae mid-anteriorly; rugose above; densely and moderately coarsely punctate below (interspaces imbricate). Lateral surface of propodeum densely and finely punctate; interspaces rugulose. Vertical surface of metapostnotum with transverse carinae above. T1–T5 sparsely and minutely punctate; interspaces smooth throughout. T6 densely and finely punctate. S1–S5 moderately densely and finely punctate (except S2–S5 sparsely punctate mid-longitudinally); interspaces imbricate throughout. S6 densely and moderately coarsely punctate (except finely punctate mid-longitudinally); interspaces imbricate (except longitudinally finely striate towards posterior margin).

MALE (Figs. 27B, 27D, 27F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 7.2–7.9; head width 2.7–3.1; head length 2.1–2.4; intertegular distance 1.9–2.3; forewing length 6.7–7.2.

*Colouration:* Front and mid tarsi, distal ring of hind tibia dark-orange. Hind femur anterodorsally pale-brown. Marginal zone of T6 pale-yellow. S2–S5 posteriorly, disc of S6 pale-brown.

*Structure:* Clypeal mid-longitudinal area moderately narrowly (0.6x MOD) depressed on upper 2/3, much broadly depressed on lower 1/3. Malar area ~1.3x as long as basal depth of mandible (38:30). F1 ~0.8x as long as its apical width (23:27). UID:LID (61:52). Horizontal surface of metapostnotum ~0.6x as long as metanotum (28:44); metapostnotal pits well-delimited; posterior transverse carina very sinuous. Posteromedial surface of front coxa with small spine. Hind basitarsus ~4.3x longer than broad (47:11). Outer rami of hind tarsal claws ~1.6x as long as inner rami (11:7). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 28A, 28B, 28C, respectively.

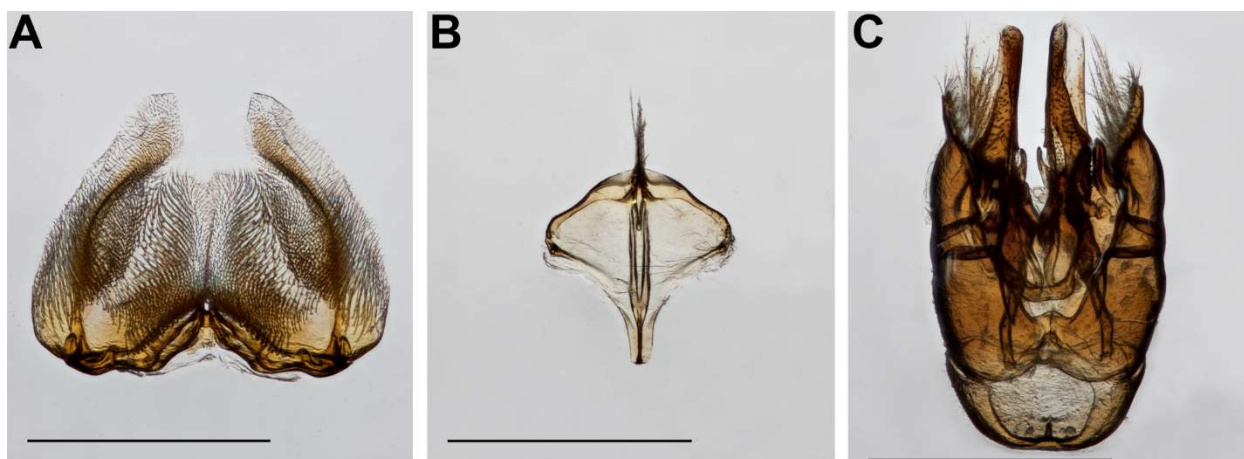
*Pubescence:* Genal area with only erect hairs. Mesosoma dorsally with pale-yellow hairs throughout. Lateral surface of propodeum with plumose, erect, long hairs. Posterior margin of hind basitarsus with long setae. T1–T5 with appressed hairs restricted to marginal zones. S3–S5 discs with moderately short setae.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and finely punctate; adjacent convex area sparsely punctate; interspaces smooth throughout. Supraclypeal area densely and moderately coarsely punctate. Vertexal area densely and moderately finely punctate throughout. Metanotum with smooth interspaces. Lateral surface of propodeum striate posteriorly. Vertical surface of metapostnotum rugose above. T1 moderately densely and moderately finely punctate. T2–T6 densely and finely punctate. Metasomal sterna minutely punctate; interspaces smooth (except imbricate anteriorly). S6 with imbricate interspaces posteriorly.

**Material studied:** *Primary type specimens:* Lectotype ♀ of *C. rufipes meridionalis* – “17.585”. “100.080”. “LECTOTYPUS; *Colletes rufipes meridionalis*; Schrottky, 1902; Ferrari & Silveira, des. 2013”. {MZSP}. Lectotype ♂ of *C. extensicornis* – “Pernambuco; Brésil”. “*Colletes* ♂; *extensicornis*; Vach”. “MUSEUM PARIS; Coll. J. Vachal 1911”. “Lectotype”. “*Colletes*; *extensicornis*; Vach.”. “MUSEUM PARIS; EY0000000465”. {MHNP}.

*Secondary type specimens:* Paralectotype ♀ of *C. rufipes meridionalis*: **BRAZIL – Rio Grande do Sul**: [H. Ihering], 1♀, {MZSP}. Paralectotype ♂ of *C. externicornis*: **BRAZIL –** 1♂, {MNHP}.

*Additional specimens:* **BRAZIL – Bahia**: Ibotirama, 18/i/1985, [Camargo], 1♀, {RPSP}. Itatim, 26/x/1996, 1♀, {MZUEFS}. **Distrito Federal**: Brasília, Campus da UnB, 18/vi/2004, [L. Pierrot], 1♀, {UFMG}. **Minas Gerais**: Araxá, 22/iv/ 1965, [C. Elias], 2♂♂, {DZUP}; idem, except 28/iv/1965, 1♀; idem, except 10/v/1965, 1♀. Bonfinópolis de Minas, 26/iii/2000, [M. Mazucato], 3♂♂, {RPSP}. Brasilândia de Minas, Fazenda Brejão, 23/vii/2000, [F. Silveira], 1♂, {UFMG}. Brazópolis, xii/1961, [C. Elias], 2♀♀8♂♂, {DZUP}. Brumadinho, Serra da Moeda, 20/xii/1998, [F. Silveira], 1♀, {UFMG}. Catas Altas, Serra do Caraça, [Kloss, Lenko, Martins & Silva], 1♂, {MEUV}. Nova Resende, vii/1961, [C. Elias], 1♂, {DZUP}. Passos, iv/1961, [C. Elias], 1♂, {DZUP}; idem, except 13/xi/1961, 1♀; idem, except 1/iii/1962, 1♂; idem, except 1/viii/1962, 1♀; idem, except 1/ix/1962, 1♀; idem, except 22/viii/1962, 1♀; idem, except 5/viii/1963, 1♀; idem, except 21/xii/1964, 1♀; idem, except 5/xi/1961, 1♀, {RPSP}. Patos de Minas, 23/xi/1965, [C. Elias], 2♂♂, {DZUP}. Patrocínio, Parque Florestal de Patrocínio, 8/xii/2007, [J. Santos], 1♀4♂♂, {UFMG}; idem, except 18/xii/2007, 1♀ 2♂♂; idem, except 4/i/2008, [J. Santos], 1♂. Poços de Caldas, xi/1961, [C. Elias], 1♀4♂♂, {DZUP}. Ritápolis, 5/i/1975, [J. Camargo], 1♀, {RPSP}. São Gonçalo do Rio Preto, Parque Estadual do Rio Preto, 31/x/2002, [F. Coelho], 4♀♀, {UFMG}; idem, except 18/ix/2003, [L. Faria], 1♀, {UFMG}. São Roque de Minas, Serra da Canastra, 26/ii/2001, [E. Almeida], 1♀, {UFMG}; idem, except 28/iii/2007, [A. Azevedo], 1♀2♂♂. Serra do Cipó, (-19.3000, -43.5833), 25/ii/1993, [G. Faris], 1♂, {RPSP}. Serra do Salitre, RPPN Cachoeira do Campo, (-19.1666, -46.5682), 2/xii/2016, [Ferrari & Hilário], 6♂♂, {PCYU}. Uberaba, x/1961, [C. Elias], 1♀1♂, {DZUP}. Uberlândia, Estação Ecológica do Panga, 24/x/2006, [A. Carvalho], 1♀, {UFMG}; idem, except 21/xi/2006, 1♂. Viçosa, Universidade Federal de Minas Gerais, 4/iii/1989, [G. Bastos], 1♀, {MEUV}; idem, except 11/iii/1989, 1♀. **Piauí**: 30km NW of Bom Jesus, (-8.9500, -44.5833), 25/i/1993, 1♀, {RPSP}. **Rio Grande do Sul**: Santana do Livramento, (-30.8730, -55.5283), 3/xi/2012, [Almeida & Aguiar], 1♀, {RPSP}. **Santa Catarina**: Nova Teutônia, (-27.1833, -52.3833), 4/iii/1949, [F. Plaumann], 1♀, {AMNH}. **São Paulo**: Altinópolis, 12/i/1978, [M. Mazucato], 1♂, {RPSP}.



**Figure 28.** Dorsal view of the male terminalia of *Colletes meridionalis*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Range:** BRAZIL (Bahia, Distrito Federal, Minas Gerais, Pernambuco, Piauí, Rio Grande do Sul, Santa Catarina, São Paulo). See also Fig. 22.

**Biogeographical distribution:** Chacoan dominion (Caatinga, Cerrado and Pampean provinces), and Parana dominion (Parana Forest province) at altitudes of 400–1500m a.s.l.

**DNA barcode:** Available. BOLD: ADF9673 (2♀♀2♂♂). Distance from the nearest neighbour (*C. rufipes*): 10.55–11.51%.

**Floral hosts:** Compositae – *Helianthus annuus* L. (Moure 1945 (as “girasol”)). Lythraceae – *Cuphea* sp. (this study). Sapindaceae – *Matayba guianensis* Aubl. (Carvalho & Oliveira 2010 (as *C. extensicornis*)).

**Comments:** Relatively common species widely distributed in Brazil (from Rio Grande do Sul state as north as Piauí state).

The synonymy of *C. extensicornis* under *C. meridionalis* by Ferrari & Silveira (2015) that was justified by the presence of a unique characteristic (mesepisternum ventrally with a protrusion surrounded by appressed short hairs) in the primary type specimens of both species is herein further supported by DNA barcoding.

***Colletes michenerianus* Moure, 1956**

(Figs. 19, 29, 30, 45B, 45D, 51C)

*Colletes micheneriana* Moure, 1956: 201.

Holotype ♀ examined. (DZUP).

*Colletes michenerianus*; Michener & Lange 1957: 77; Michener *et al.* 1958b: 208; Torchio 1965: 187; Graf 1967: 129, 1968: 73; McGinley 1981: 90; Torchio *et al.* 1988: 620; Schlindwein 1995: 88, 1998: 51; Moure & Urban 2002: 13; Silveira *et al.* 2002: 155; Moure *et al.* 2007: 684, 2012; Ascher & Pickering 2018.

*Colletes mochinerianus* (sic); Michener *et al.* 1958a: 4.

**Diagnosis:** Both sexes of *C. michenerianus* can be diagnosed through the combination of mesoscutum with off-white and black hairs intermixed, legs with fuscous to black hairs, and T1–T5 discs metallic-blue. *Colletes michenerianus* is most similar to *C. cyaneus* as in both species T1–T5 discs are metallic-blue, characteristic of which is unique amongst the species of the genus found in southern Brazil. However, their females can be differentiated from one another by labrum medially concave in *C. michenerianus* (labrum medially convex in *C. cyaneus*); and scopa with fuscous hairs in *C. michenerianus* (scopa with pale-yellow hairs in *C. cyaneus*). The males of the two species can be distinguished by malar area relatively short, ~1.5x as long as basal depth of mandible, in *C. michenerianus* (malar area ~1.8x as long as basal depth of mandible in *C. cyaneus*); and legs with fuscous hairs in *C. michenerianus* (legs with off-white hairs in *C. cyaneus*).

**Redescription:** FEMALE (Figs. 29A, 29C, 29E):

*Dimensions (mm):* Approximate body length 9.8–10.2; head width 3.5–3.7; head length 2.7–2.8; intertegular distance 2.9–3.1; forewing length 8.1–8.4.

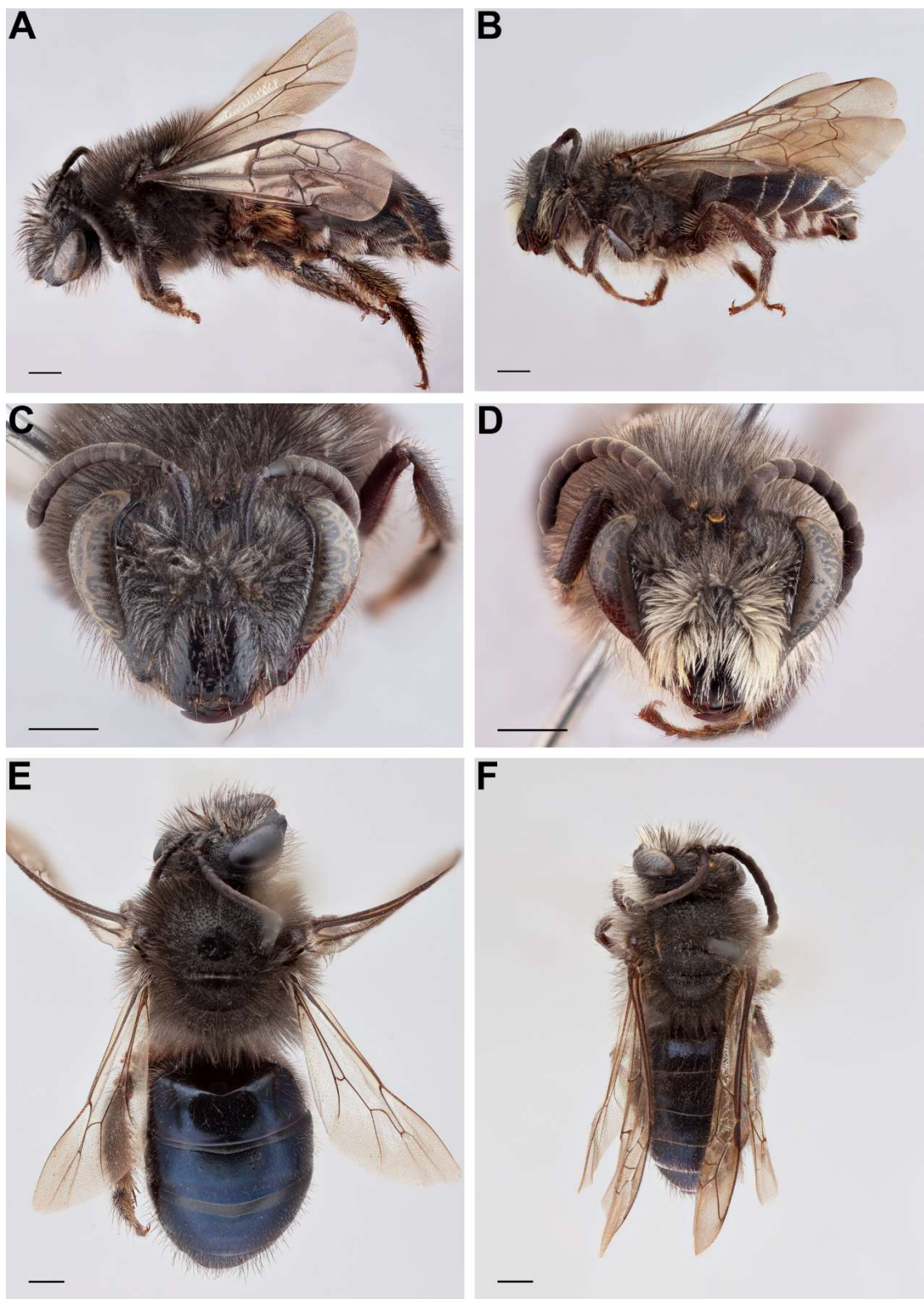
*Colouration:* Black except T1–T5 (except marginal zones dark-brown with purplish reflections) metallic dark-blue. Distal 1/3 of mandible, distal half of tarsal claws reddish-brown. Ventral surface of F2–F5, tegula, wing venation (except veins R and C of forewing black), stigma, dorsal surface of tarsi (except basitarsi black), posteroventral surface of mid and hind femora, posterior surface of hind tibia, ventrally inflexed lateral areas of T1–T4, S1–S5



posteriorly, S6 mid-longitudinally dark-brown. Proximal half of tarsal claws, marginal zones of S1–S5 pale-brown.

*Structure:* Labrum medially convex; convexity not margined laterally by lateral ridges. Clypeal mid-longitudinal area shallowly and narrowly (0.4x MOD) depressed on upper half. Malar area ~1.1x as long as basal depth of mandible (48:45). Hypostomal carina short and flat. F1 ~1.5x as long as its apical width (46:30). UID:LID (69:68). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum pointed. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum ~0.4x as long as metanotum (19:46); metapostnotal pits poorly-delimited; posterior transverse carina sinuous and incomplete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.2x longer than broad (51:16). Outer rami of hind tarsal claws ~2.2x as long as inner rami (13:6). Marginal zone of T1 flat. Marginal zone of S6 depressed.

*Pubescence:* Head with plumose, erect, long, off-white and black hairs intermixed; except mandible with fuscous setae; genal area with short hairs near outer margin of eye. Mesosoma with black, plumose, erect, long hairs; pronotal lobe and mesoscutum with black long hairs and off-white moderately long hairs intermixed; mesepisternum and metepisternum with very long hairs; lateral surface of propodeum with off-white, suberect, moderately short hairs posteriorly. Legs with fuscous, erect, moderately long setae (except femoral and tibial scopae with pale-yellow, branched apically only, suberect, very long hairs anteriorly); trochanters and femora with black, plumose, erect, long hairs anteroventrally; front and mid tibiae with suberect, short setae anterodorsally (except mid tibia with erect setae anteriorly); posterior margins of basitarsi and posterior surface of hind tibia with long setae (those setae very long on mid and hind basitarsi). Metasoma terga with fuscous, suberect, short setae; except T1 with plumose, erect, moderately long hairs; T4–T5 with black, erect, long setae laterally; T6 covered with black, suberect, moderately long setae. Metasomal sterna with fuscous, suberect, moderately short setae; except S1 with plumose, erect, long hairs; S2 with branched apically only, erect, moderately long hairs; S3–S5 with minute setae anteriorly; S2–S5 marginal zones with a transverse line of pale-yellow, plumose, suberect, moderately short hairs.



**Figure 29.** *Colletes michenerianus* Moure, 1956. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.

*Surface sculpture:* Clypeal mid-longitudinal depression densely and moderately coarsely punctate (interspaces imbricate above, smooth below); adjacent convex area sparsely punctate (interspaces smooth throughout). Supraclypeal area imbricate. Malar area with fine, collapsing punctures above (interspaces rather finely striate); substrigulate near mandibular base. Paraocular area densely and moderately finely punctate (except punctures coarser towards clypeus and sparser near antennal socket); interspaces imbricate. Frontal area densely and moderately coarsely punctate; interspaces imbricate. Vertexal area sparsely and finely punctate near eye (interspaces smooth, except imbricate posteriorly); punctures crowded and moderately fine near lateral ocellus. Mesosoma with imbricate interspaces, except when stated otherwise. Mesoscutum and scutellum densely and coarsely punctate (except mesoscutum posteromedially and scutellum anteriorly with sparse punctures). Metanotum densely and moderately coarsely punctate; punctures poorly-delimited, interspaces rugose. Mesepisternum densely and coarsely punctate (except punctures crowded below scrobe). Metepisternum with oblique carinae mid-anteriorly; densely and moderately coarsely punctate above and below. Lateral surface of propodeum sparsely and finely punctate. Vertical surface of metapostnotum rugose above. Metasoma with imbricate interspaces throughout. T1–T5 sparsely and minutely punctate. T6 moderately densely and finely punctate. S1 sparsely and finely punctate. S2–S4 moderately densely and finely punctate (except sparsely punctate mid-longitudinally and densely punctate posteriorly). S5–S6 densely and moderately finely punctate.

MALE (Figs. 29B, 29D, 29F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.0–8.5; head width 3.0–3.3; head length 2.5–2.7; intertegular distance 2.2–2.5; forewing length 7.2–7.7.

*Colouration:* Ventral surface of flagellum black. Hind leg dark-brown (except dorsal surface of hind distitarsus pale-brown). T6 metallic dark-blue. S6 disc entirely dark-brown.

*Structure:* Clypeal mid-longitudinal area shallowly depressed throughout; depression relatively narrow (0.6x MOD) above, much broader (1.5x MOD) below. Malar area ~1.5x as long as basal depth of mandible (46:30). F1 ~1.1x as long as its apical width (28:26). UID:LID (66:61). Horizontal surface of metapostnotum ~0.4x as long as metanotum (17:41); metapostnotal pits well-delimited. Hind basitarsus ~4.1x longer than broad (53:13). Outer rami

of hind tarsal claws ~1.6x as long as inner rami (11:7). Marginal zone of S6 not depressed. S7, S8 and genitalia as in Figs. 30A, 30B, 30C, respectively.

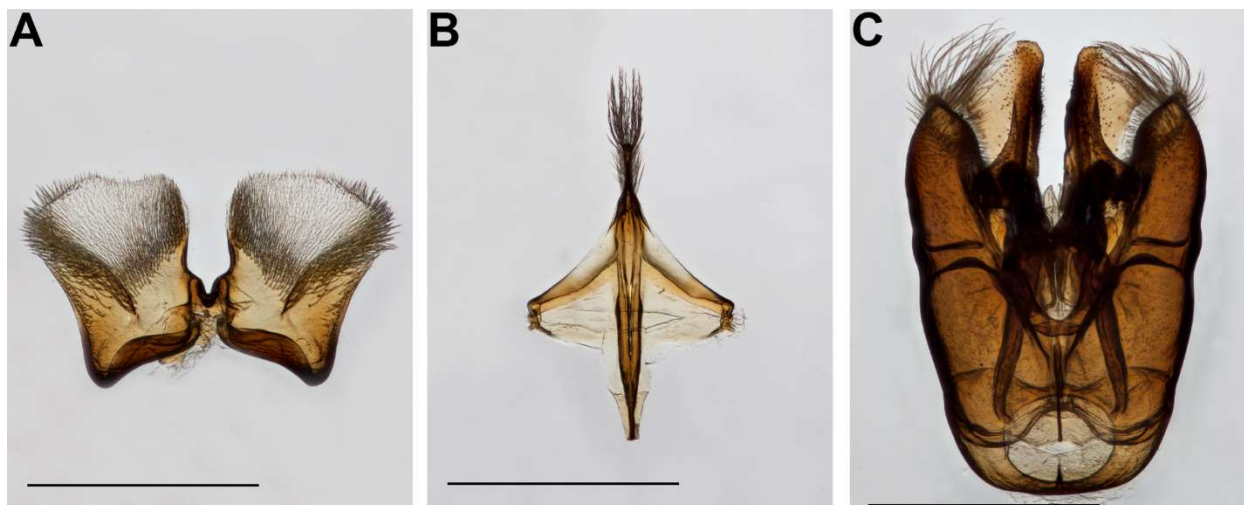
*Pubescence*: Mandible with pale-yellow setae. Clypeus, supraclypeal area and paraocular area near clypeus with off-white hairs only. Genal area with pale-yellow, very long hairs towards proboscideal area. Vertexal area with black, very long hairs near occipital area. Mesosomal hairs as long as those on mesepisternum. Metanotum with very long hairs. Lateral surface of propodeum with black, erect hairs throughout. Legs with pale-yellow hairs (except front and mid femora and tibiae with fuscous hairs posteriorly). T1 with black, plumose, erect, long hairs; those hairs moderately short on T2. T1–T5 marginal zones with narrow band of off-white, plumose, appressed, short hairs; bands interrupted medially on T1–T4, complete on T5–T6. Metasomal sterna discs with pale-yellow hairs; S2 with plumose hairs; S3–S5 with moderately short setae anteriorly, those setae moderately long laterally.

*Surface sculpture*: Clypeus with convex area largely impunctate. Malar area substrigulate throughout. Paraocular area with rugulose interspaces above. Frontal area punctures crowded. Vertexal area densely and moderately finely punctate near eye; interspaces rugulose. Mesosoma moderately densely punctate; punctures poorly-delimited; interspaces rugulose. Mesepisternum sparsely punctate towards ventral surface. T1–T6 sparsely and finely punctate. S2–S4 evenly moderately sparsely punctate. S6 sparsely and finely punctate.

**Material studied:** *Primary type specimen*: Holotype ♀ – “HOLOTIPO”. “GUARAPUAVA 1120; Paraná BRASIL; 7-IX-1955; Michener e Moure”. “michenerianus”. {DZUP}.

*Secondary type specimens*: Allotype ♂: **BRAZIL – Paraná**: Guarapuava, 7/ix/1955, [Michener & Moure], {DZUP}. Paratypes ♀♀ and ♂♂: **BRAZIL – Paraná**: Curitiba, x/1944, [J. Moure], 1♀, {DZUP}; idem, except viii/1954, [J. Moure], 2♂♂; idem, except viii/1955, [R. Lange], 1♂. Curitiba-Paranaguá Highway km 8, 14/ix/1955, [Lange, Michener & Moure], 1♂, {DZUP}. Guarapuava, 7/ix/1955, [Michener & Moure], 1♂, {DZUP}; idem, except 1♀1♂, {SEMC}.

*Additional specimens*: **BRAZIL – Paraná**: Curitiba, , [S. Laroca], 11/ix/1963, 1♂, {SEMC}; idem, except 1/x/1963, 1♀. Palmas, (-26.5570, -51.5420), 21/ix/2012, [Pereira-Rocha], 1♂, {DZUP}.



**Figure 30.** Dorsal view of the male terminalia of *Colletes michenerianus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Range:** Brazil (Paraná). See also Fig. 19.

**Biogeographical distribution:** Paraná dominion (*Araucaria* Forest province) at altitudes of 800–1200m a.s.l.

**DNA barcode:** Unavailable.

**Floral hosts:** Berberidaceae – *Berberis laurina* Thunb. (Schlindwein 1995, 1998). Leguminosae – *Prosopis* sp. (this study).

**Comments:** Rare species seemingly associated with the *Araucaria* Forest in Southern Brazil.

Moure (1956) raised the question that *C. michenerianus* could be but a subspecies of *C. cyaneus*, even though he had listed a few characteristics (e.g. sculpture of labrum and malar area length) that could be used to distinguish the two forms from each other (see Moure 1956: 203). Indeed, the characters mentioned by Moure coupled with those listed in the “Diagnosis” (see above) support the status of *C. michenerianus* as a valid, separate species.

***Colletes ornatus* Schrottky, 1902**

(Figs. 31, 32, 33)

*Colletes ornatus* Schrottky, 1902: 345; Ducke 1907: 75; Schrottky 1907: 8, 1913: 236; Friese 1916: 290, 1921: 77; Moure & Urban 2002: 16; Silveira *et al.* 2002: 155; Moure *et al.* 2007: 685; Rasmussen *et al.* 2009: 33; Gonçalves *et al.* 2012: 55; Moure *et al.* 2012; Ferrari & Silveira 2015: 264; Ramos *et al.* 2015: 349; Ascher & Pickering 2018.

Holotype ♀ examined. (MZUSP).

**Diagnosis:** *Colletes ornatus* can be easily diagnosed by mesoscutum anterolaterally and pronotal lobe covered with distinctive patch of bright-orange (pale-yellow in the male) hairs that strongly contrast with pale-yellow (off-white in the male) sparse pubescence elsewhere on dorsum of mesosoma; characteristic of which is visible even to the naked eye. *Colletes ornatus* resembles *C. rugicollis* in that in both the hypostomal carina is produced as a tall, concave lamella in profile. However, the two species can be easily differentiated from each other by pubescence mostly light in *C. ornatus* (pubescence mostly dark in *C. rugicollis*), and T1 moderately finely punctate in *C. ornatus* (T1 coarsely punctate in *C. rugicollis*).

**Redescription:** FEMALE (Figs. 31A–C):

*Dimensions (mm):* Approximate body length 9.4–10.1; head width 3.1–3.3; head length 2.3–2.5; intertegular distance 2.2–2.5; forewing length 6.9–7.4.

*Colouration:* Black except distal half of mandible, clypeus towards lower margin, distal 2/3 of tarsal claws, S6 posterolaterally reddish-brown. Tegula pale-orange. Wing venation (except veins C and R of forewing black), legs (except pale-brown on distal rings of front and mid distitarsi and hind tarsus), marginal zones of T1–T5, discs of S2–S5 dark-brown. Stigma, proximal 1/3 of tarsal claws pale-brown. Tibial spurs, marginal zones of metasomal sterna pale-yellow.

*Structure:* Labrum medially concave; concavity margined laterally by longitudinal ridges. Clypeal mid-longitudinal area deeply and broadly (0.8x MOD) depressed, except depression much narrower (0.2x MOD) above. Malar area ~0.9x as long as basal depth of mandible (40:46). Hypostomal carina produced as a tall, concave lamella in profile. F1 slightly longer than its



apical width (28:27). UID:LID (57:54). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum modified into a long spine. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by short hairs. Horizontal surface of metapostnotum 0.8x as long as metanotum (40:50); metapostnotal pits well-delimited; posterior transverse carina somewhat sinuous and complete. Posteromedial surface of front coxa with weak spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.7x longer than broad (66:18). Outer rami of hind tarsal claws ~1.5x as long as inner rami (14:9). Marginal zone of T1 flat. Marginal zone of S6 depressed.

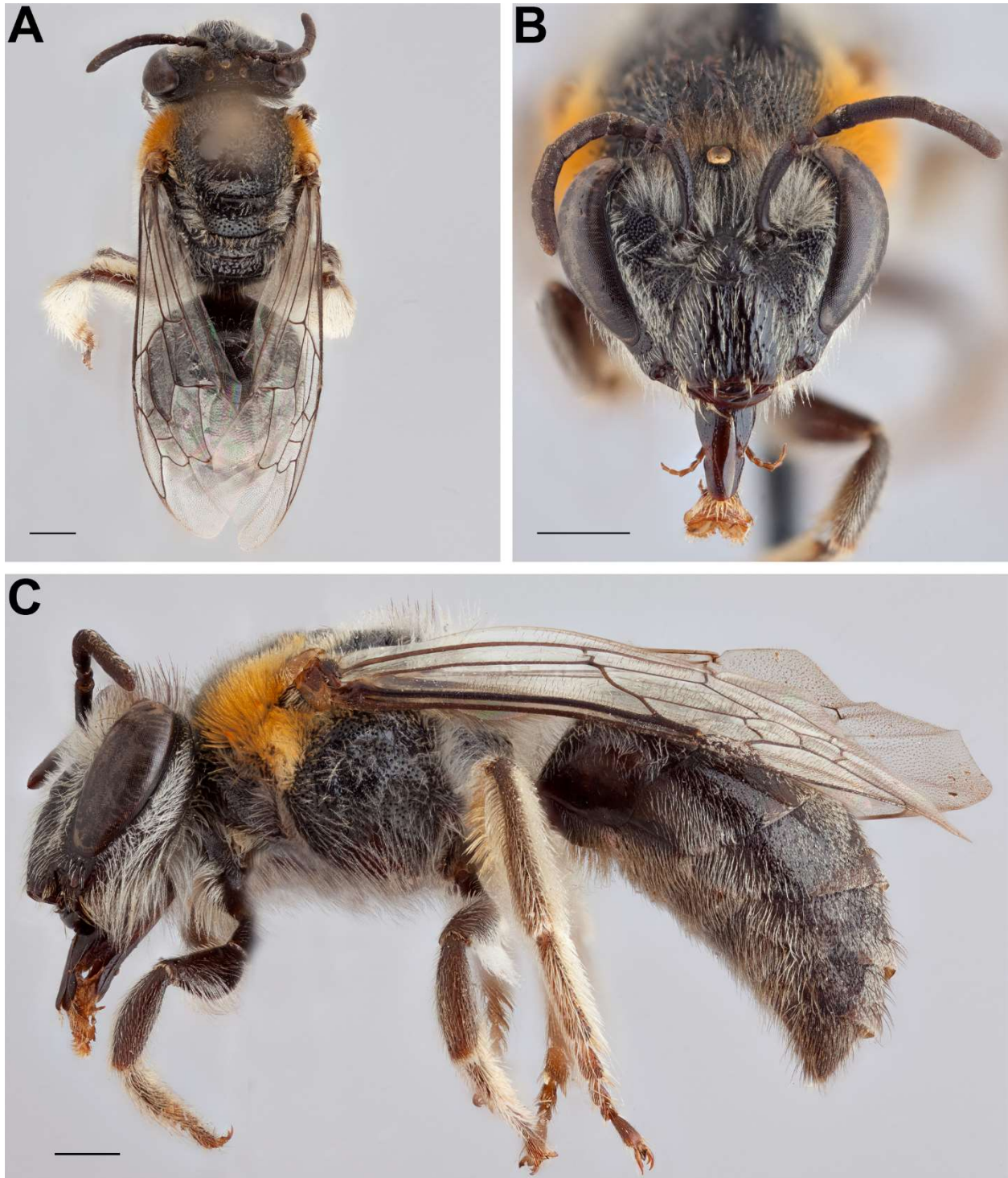
*Pubescence:* Head with off-white, plumose, erect, moderately short hairs; except mandible and labral lower margin with pale-yellow setae; paraocular area with off-white and black hairs intermixed; frontal area with fuscous, moderately long hairs; genal area with appressed hairs adjacently to outer margin of eye and long hairs towards proboscis fossa; vertexal area with black, long hairs. Mesosoma with off-white, plumose, erect hairs; those hairs short on mesoscutum and scutellar anterior half, moderately long elsewhere (except upper margin of lateral surface of propodeum with fuscous, very long hairs); mesoscutum anterolaterally and pronotal lobe with distinctive patch of bright-orange hairs that contrasts strongly with pale hairs elsewhere on dorsum of mesosoma; scutellum with off-white and fuscous hairs intermixed towards posterior margin; lateral surface of propodeum with appressed, short hairs on disc. Legs with pale-yellow hairs (except posterior surface of mid femur and posterior margin of hind tibia with fuscous setae); trochanters and femora with plumose, erect, long hairs (mid femur with short setae on anteroventral surface proximally); femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; tibiae with suberect, short setae (except hind tibiae with erect, moderately short setae posterodorsally); basitarsi with erect, moderately short setae (posterior margins with long setae). Metasomal terga with off-white, plumose, appressed, short hairs (except T6 with black, suberect, moderately short setae); T1 also with off-white, plumose, erect, long hairs; T2–T5 with erect setae laterally (pale-yellow short setae on T2–T3, black moderately short on T4–T5). Metasomal sterna with pale-yellow hairs; S1 with plumose, erect, moderately long hairs; S2–S6 with suberect, short setae on discs (except S5 with moderately short setae posteromedially); S2–S4 with a line a plumose, suberect, moderately short hairs near marginal zones.

*Surface sculpture:* Clypeus moderately coarsely punctate; lower 2/3 moderately densely punctate, upper 1/3 sparsely punctate; integument longitudinally finely striate near lower margin; interspaces smooth throughout. Supraclypeal area sparsely and moderately finely punctate; interspaces imbricate. Malar area densely and moderately finely punctate (except punctures finer near lower summit of eye); punctures ill-defined and coalescent with striate interspaces. Paraocular area densely and moderately finely punctate (punctures sparser and coarser towards antennal socket); interspaces smooth. Frontal area densely and moderately coarsely punctate; interspaces imbricate. Vertexal area densely and moderately finely punctate (except finely punctate near eye); interspaces smooth. Mesoscutum moderately sparsely and moderately coarsely punctate (except densely punctate antero-laterally and sparsely punctate posteromedially); interspaces smooth throughout. Scutellum coarsely punctate; anterior half moderately sparsely punctate (interspaces smooth); posterior half densely punctate (interspaces rugulose). Metanotum densely and moderately finely punctate; interspaces rugulose. Mesepisternum moderately densely and moderately coarsely punctate (except densely punctate anterior to episternal groove and near scrobe); interspaces smooth (except rugulose anterior to episternal groove). Metepisternum with oblique carinae anteriorly; rugose above; densely and moderately coarsely punctate below (interspaces rugulose). Lateral surface of propodeum sparsely and finely punctate; interspaces imbricate. Vertical surface of metapostnotum rugose above. Metasomal terga with smooth interspaces throughout; T1 moderately densely and moderately finely punctate (except finely punctate towards marginal zone), T2 andesely and finely punctate throughout; T3–T5 moderately densely and minutely punctate. Metasomal sterna with imbricate interspaces throughout; S2–S5 moderately finely punctate, punctuation sparsest on S2, densest on S5; S6 densely and moderately finely punctate anteriorly, punctures somewhat coarser but difficult to discern posteriorly.

MALE. As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.2–9.0; head width 2.5–2.7; head length 2.1–2.2; intertegular distance 1.7–1.9; forewing length 6.5–6.8.

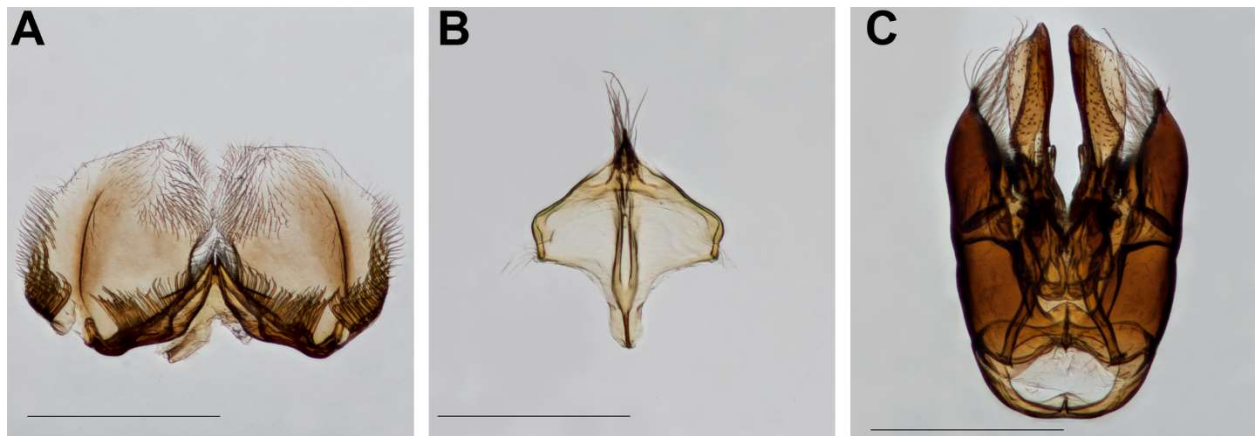
*Colouration:* Mandible proximally dark-brown, distally dark-orange. Legs pale-brown (except coxae, trochanters, front and mid femora, front and mid tibiae posterodorsally dark-brown). S6 dark-brown.



**Figure 31.** *Colletes ornatus* Schrottky, 1902. Female: (A) habitus, dorsal view; (B) face, frontal view; (C) habitus, lateral view. Scale bars = 1mm.

*Structure:* Clypeal mid-longitudinal depression shallow throughout; depression relatively narrow (0.3x MOD) on upper half, much broader below (maximum width 1.2x MOD). Malar area ~1.8x as long as basal depth of mandible (52:28). F1 ~0.9x as long as its apical width (23:25). UID:LID (66:50). Anterolateral angle of pronotum pointed. Horizontal surface of metapostnotum ~0.7x as long as metanotum (38:52); posterior transverse carina very sinuous. Posteromedial surface of front coxa without spine. Hind basitarsus ~3.8x longer than broad (46:12). Outer rami of hind tarsal claws ~1.3x as long as inner rami (18:14). Marginal zone of S6 not depressed posteriorly. S7, S8 and genital capsule as in Figs. 32A, 32B, 32C, respectively.

*Pubescence:* Frontal area with off-white, long hairs. Genal area with erect hairs only. Vertexal area with off-white and fuscous, long hairs intermixed. Distinctive patch on mesoscutum anterolaterally and pronotal lobe with pale-yellow hairs; mesosoma dorsally with off-white hairs elsewhere. Lateral surface of propodeum with erect hairs on disc. Mid femur and hind tibiae with pale-yellow setae posteriorly. Metasomal terga with appressed, short hairs restricted to marginal zones (except T6); T2 with pale-yellow, plumose, erect, moderately long hairs on disc; T3–T6 with fuscous, suberect, minute setae on disc (except T5–T6 with intermixed minute and moderately short setae). S2 with plumose, erect, short hairs. S3–S6 with short setae on discs. S5 with a line a plumose, suberect, moderately short hairs near marginal zone.



**Figure 32.** Dorsal view of the male terminalia of *Colletes ornatus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Surface sculpture:* Clypeus with convex area sparsely punctate; mid-longitudinal depression densely punctate. Supraclypeal area with rugulose interspaces. Malar area densely and moderately coarsely punctate. Paraocular area evenly densely and moderately finely punctate. Vertexal area punctures crowded. Mesoscutum with rugulose interspaces anteriorly and imbricate interspaces posteriorly. Scutellum sparsely punctate; interspaces smooth throughout. Mesepisternum evenly coarsely punctate; interspaces anterior to episternal groove imbricate. Lateral surface of propodeum rugose. T1 densely punctate. T2 moderately finely punctate. S2–S5 sparsely and finely punctate (except S4 posteriorly and S5 moderately densely punctate).

**Material studied:** *Primary type specimen:* Holotype ♀ – “17.586”. “100.075”. “Colletes ♀; ornatus Schr.; P. Moure det.39”. “BRASIL, SÃO PAULO; JUNDIAÍ; Staudinger col.”. “HOLOTYPE; Colletes ornatus ♀; Schrottky, 1902; labelled R. Ferrari, 2018”. {MZUSP}.

*Additional specimens:* **BRAZIL – Mato Grosso:** Tapirapé Indian Village, Confluence of Rivers Tapirapé and Araguaia, 11/xi/1960, [B. Malkin], 5♀♀, {FMNH}; idem, except 10/xii/1960, 1♀; idem, except 15/xii/1960, 1♀. Rio Caraguata, iii/1953, [F. Plaumann], 1♀, {SEMC}. **Minas Gerais:** Brazópolis, xii/1961, [C. Elias], 3♂♂, {DZUP}. Uberaba, x/1961, [C. Elias], 4♂♂, {DZUP}. **Pará:** Serra dos Gradaús, 20/viii/1983, [Camargo], 1♀, {RPSP}. **Santa Catarina:** Nova Teutônia, 7/xii/1953, [F. Plaumann], 1♀, {SEMC}. **PARAGUAY – Caaguazú:** unspecified locality, xi/1950, [F. Schade], 1♀, {SEMC} **Guairá:** Paso Yobái, iv/1951, [F. Schade], 1♂, {SEMC}; idem, except 8/xi/1951, [J. Foerster], 1♂. **San Pedro:** San Estanislao, xii/1945, [Bridarolli], 1♀, {SEMC}.

**Range:** ARGENTINA (Misiones), BRAZIL (Mato Grosso, Minas Gerais, Pará, Santa Catarina, São Paulo), PARAGUAY (Caaguazú, Guairá, San Pedro). See also Fig. 33.

**Biogeographical distribution:** Chacoan dominion (Cerrado and Chacoan provinces), Parana dominion (*Araucaria* and Parana Forest provinces), and South eastern Amazonian dominion (Xingu-Tapajós province) at altitudes of 100–1000m a.s.l.

**DNA barcode:** Unavailable.





**Figure 33.** Geographical distribution of *Colletes ornatus* (blue circles), and *C. sexangulus n. sp.* (red stars). Scale bar approximately 250km.

**Floral hosts:** Unknown.



**Comments:** Uncommon species yet widely distributed in eastern South America. *Colletes ornatus* has been recorded as far north as San José in Costa Rica (Friese 1916), but I was unable to verify this report.

***Colletes pampeanus* Ferrari, new species**

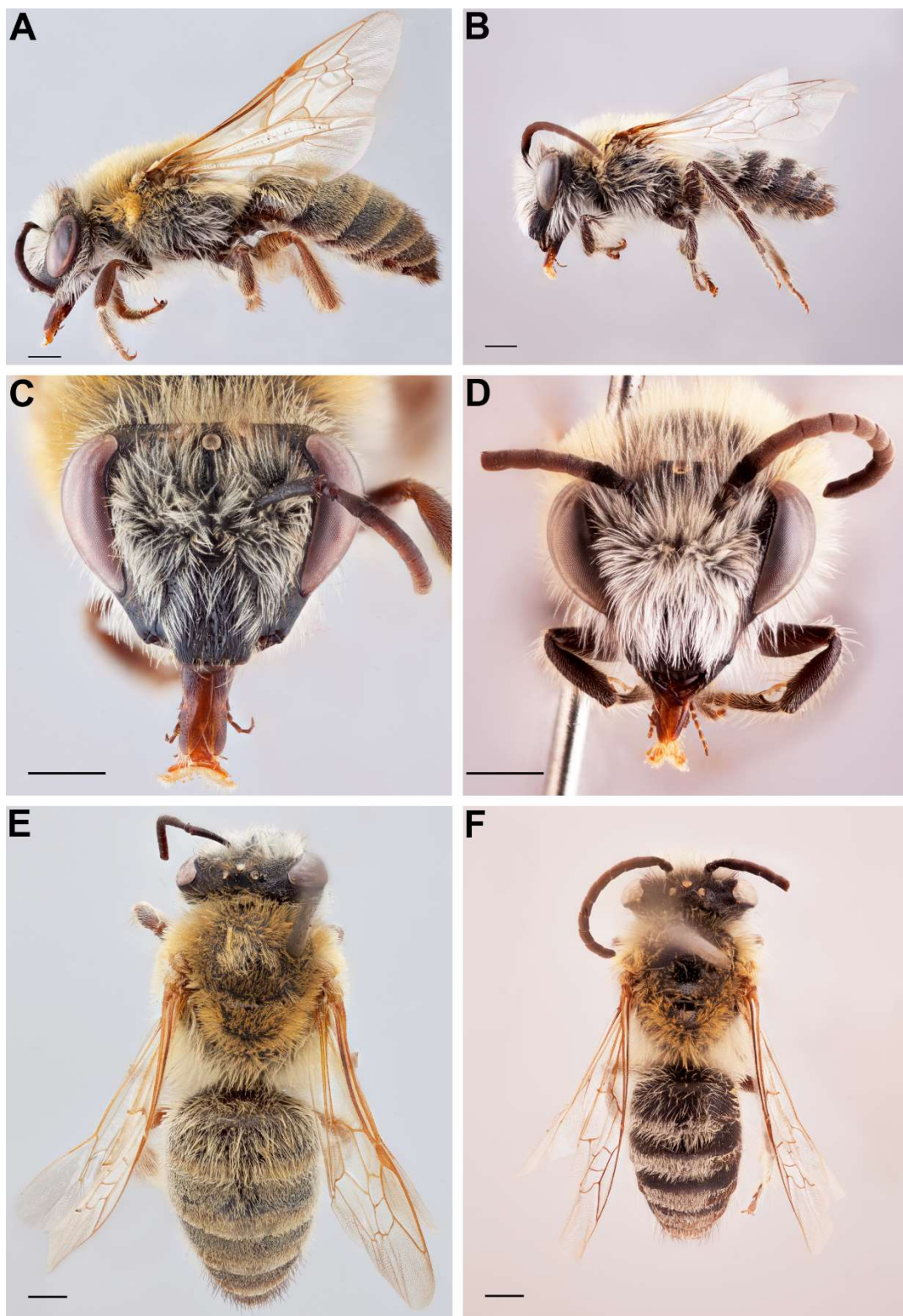
(Figs. 4, 34, 35)

**Diagnosis:** The female of *C. pampeanus* **n. sp.** can be diagnosed through the combination of labrum black and concave medially, clypeal convex area longitudinally finely striate, and mesoscutum covered with pale-yellow hairs. The male is diagnosable by paraocular area with pale-yellow and black hairs intermixed, and T3–T5 discs with erect setae and marginal zones with appressed hairs. *Colletes pampeanus* **n. sp.** is most similar to *C. meridionalis* as both are virtually the same size (10/8mm in length (♀/♂)), and have legs covered with pale-yellow setae and metasomal terga with pale-yellow appressed hairs. The two species, however, can be differentiated from one another by mesepisternum without protrusion ventrally in *C. pampeanus* **n. sp.** (mesepisternum ventrally with protrusion surrounded by appressed short hairs, in *C. meridionalis*); and malar area considerably longer, ~1.2/2.0x MOD (♀/♂), in *C. pampeanus* **n. sp.** (malar area ~0.6/~1.3x MOD (♀/♂) in *C. meridionalis*).

**Description:** FEMALE (Figs. 34A, 34C, 34E):

*Dimensions (mm):* Approximate body length 10.3; head width 3.4; head length 2.6; intertegular distance 2.5; forewing length 7.4.

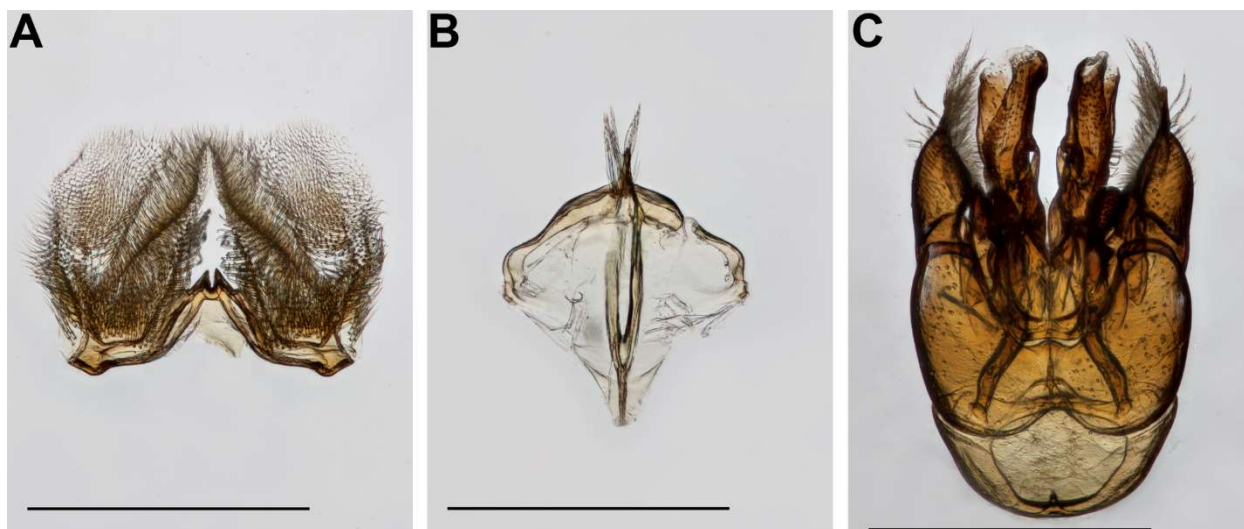
*Colouration:* Black except mandible, malar area below, clypeal convex area, apical ring of scape, pedicel, F1–F2 ventrally reddish-brown. Tegula, wing venation (except vein R of forewing black), stigma, legs (except front basitarsus black, coxae and trochanters dark-brown, distitarsi and proximal half of tarsal claws dark-yellow), marginal zones of T1–T5 pale-brown. Ventral surface of F3–F10, ventrally reflexed lateral areas of T1–T5, discs of S2–S6 (except S3–S5 marked with pale-brown posteromedially and S6 mid-longitudinally) dark-brown. Tibial spurs, marginal zones of metasomal sterna pale-yellow.



**Figure 34.** *Colletes pampeanus* n. sp. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.

*Structure:* Labrum medially concave; concavity margined laterally by longitudinal ridges. Clypeal mid-longitudinal area deeply depressed throughout; depression narrowest above (0.4x MOD), broadest below (2x MOD). Malar area ~1.2x as long as basal depth of mandible (45:38). Hypostomal carina short and flat. F1 ~1.3x as long as its apical width (40:30). UID:LID (67:61). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum modified into a long spine. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum ~0.5x as long as metanotum (25:49); metapostnotal pits well-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.5x longer than broad (57:16). Outer rami of hind tarsal claws ~1.7x as long as inner rami (15:9). Marginal zone of T1 flat. Marginal zone of S6 depressed.

*Pubescence:* Head with off-white, plumose, erect, moderately long; except paraocular area with off-white and black hairs intermixed; genal area with very long hairs towards proboscidal fossa; frontal and vertexal areas with fuscous, long hairs. Mesosoma with pale-yellow, plumose, erect, long hairs; except pronotal lobes and mesoscutum with moderately long hairs; mesepisternum and metepisternum with off-white hairs; lateral surface with appressed short hairs on disc, very long hairs on upper margin. Legs with pale-yellow hairs; trochanters and femora with plumose, erect, long hairs (except front trochanter and femur with plumose hairs and setae intermixed); front and mid tibiae with short, suberect setae (except ventral and posterior surfaces with erect, longer setae distally); femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; hind tibia and basitarsi with erect, moderately long setae (except posterior margins with longer setae, longest on hind basitarsi). Metasomal terga covered with off-white, appressed, short hairs (except T6 with black, suberect, moderately short setae); T1 also with erect, plumose, long hairs (such hairs suberect and short laterally); T2–T3 also with pale-yellow, erect, moderately short setae (those setae longer laterally and posteriorly); T4–T5 also with fuscous, erect, moderately long setae (those setae pale-yellow laterally). Metasomal sterna covered with pale-yellow hairs throughout; S1 with plumose, erect, long hairs; S2 disc with erect, branched apically only, moderately long hairs; S3–S6 discs with erect, short setae (except S3–S5 with moderately long setae posteriorly); S6 setae distributed mid-longitudinally; S2–S5 also with a line of plumose, suberect, moderately short hairs near marginal zones.



**Figure 35.** Dorsal view of the male terminalia of *Colletes pampeanus* n. sp. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Surface sculpture:* Clypeal convex area longitudinally finely striate; mid-longitudinal depression densely and moderately finely punctate above, sparsely punctate below. Supraclypeal area rugulose. Malar area sparsely and finely punctate near lower summit of eye; longitudinally striate medially; substrigulate near mandible. Paraocular area densely punctate; moderately coarsely punctate below; punctures finer above; interspaces smooth throughout. Frontal area densely and coarsely punctate; interspaces smooth. Vertexal area with minute and moderately fine punctures intermixed near eye; punctures denser and coarser towards lateral ocellus; interspaces smooth throughout. Mesoscutum densely and coarsely punctate (except punctures sparse posteromedially); interspaces smooth. Scutellum densely and moderately coarsely punctate (except punctures crowded and fine posteriorly). Metanotum punctures crowded and moderately fine; interspaces rugose. Mesepisternum densely and coarsely punctate (except punctures sparser and finer towards ventral surface); interspaces smooth (except rugulose near mid coxa). Metepisternum with oblique carinae mid-anteriorly; rugose above; densely and moderately coarsely punctate below (interspaces rugulose). Lateral surface of propodeum sparsely and moderately finely punctate (interspaces rugulose). Vertical surface of metapostnotum with transverse carina above. T1–T5 minutely punctate (interspaces smooth); T6 sparsely and finely punctate; interspaces imbricate. Metasomal sterna with imbricate interspaces

throughout; S1 minutely punctate; S2–S5 sparsely and finely punctate (punctures denser and finer towards marginal zones); S6 densely and moderately finely punctate (except punctures sparse anterolaterally).

MALE (Figs. 33B, 33D, 33F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm)*: Approximate body length 8.1; head width 3.1; head length 2.5; intertegular distance 2.4; forewing length 6.8.

*Colouration*: Reddish-brown spot on mandible restricted to distal 1/3. Malar area, clypeus black. Ventral surface of F2 dark-brown. Wing venation pale-yellow (except forewing veins C pale-brown and R dark-brown). Legs dark-brown (except dorsal surface of distitarsi pale-brown). Discs of metasomal sterna black.

*Structure*: Clypeal mid-longitudinal area shallowly and narrowly (0.7x MOD) depressed throughout. Malar area ~2x as long as basal depth of mandible (62:30). F1 as long as its apical width (26:26). UID:LID (67:61). Dorsolateral angle of pronotum pointed. Horizontal surface of metapostnotum 0.5x as long as metanotum (27:54). Hind basitarsus 3.8x longer than broad (57:15). Outer rami of hind tarsal claws ~1.6x as long as inner rami (13:8). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 35A, 35B, 35C, respectively.

*Pubescence*: Vertexal area with off-white towards occipital area, fuscous hairs near lateral ocellus. Mesoscutal hairs as long as those on scutellum and metanotum. Lateral surface of propodeum with erect, long hairs on disc. T1–T5 with appressed hairs restricted to marginal zones. T2 and S2 discs with plumose, erect, moderately long hairs. S3–S6 discs with moderately short setae. S6 with short setae (except setae long posterolaterally).

*Surface sculpture*: Clypeal convex area smooth, striation restricted to lower 1/5. Supraclypeal area densely and moderately finely punctate (except punctures sparse medially); interspaces rugulose. Paraocular area finely punctate throughout. Vertexal area moderately coarsely punctate towards occipital area. Mesoscutum moderately coarsely punctate; punctures moderately dense posteromedially. Mesepisternum moderately sparsely punctate (except densely punctate anterior to episternal groove and below scrobe). T1 densely punctate; fine and moderately fine punctures intermingled. T2–T3 moderately densely and finely punctate. T6 minutely punctate. Metasomal sterna minutely punctate throughout.

**Type material:** *Holotype* ♀ – “PINHEIRO RS; MACHADO; Brasil 30.12.1990; C. Schlidwein leg.”. “S146 H:469; F:52 1500”. “Moure det.; 4.1994”. “CCDC-30383 C10”. “HOLOTYPE; *Colletes pampeanus* ♀; Ferrari, new species”. {UFMG}.

*Paratypes:* **BRAZIL – Rio Grande Sul:** Pinheiro Machado, 2/xii/1993, [C. Schlindwein], 2♂♂, {UFMG}.

**Range:** BRAZIL (Rio Grande do Sul). See also Fig. 4.

**Biogeographical distribution:** Chacoan dominion (Pampean province) at altitudes of 300–500m a.s.l.

**DNA barcode:** Unavailable.

**Floral hosts:** Unknown.

**Etymology:** Reference to the fact that the species is currently known only from the Pampas—an important ecoregion in southeastern South America that is characterized by the predominance of grassy prairies.

**Comments:** Apparently a rare species.

***Colletes petropolitanus* Dalla Torre, 1896**

(Figs. 14, 36, 37, 46B, 46D, 48B, 54B)

*Colletes senilis* Smith, 1879: 3 (junior homonym of *Colletes senilis* Eversmann, 1852); Cockerell 1912: 565.

Lectotype ♀ examined. Designated by Moure & Urban (2002: 17). (NHMUK).  
*Colletes petropolitanus* Dalla Torre, 1896: 43 (new name for *Colletes senilis* Smith (not Eversmann)); Schrottky 1902: 346, 1907: 6; Ducke 1910a: 80, 1910b: 44; Cockerell 1917a: 438; Moure 1942: 296, 1948: 313, 1949: 437; Roig-Alsina 1991: 259; Cure *et al.* 1992: 230; Moure & Urban 2002: 17; Silveira *et al.* 2002: 155; Steiner *et al.* 2006: 7, 2010: 23; Moure *et al.* 2007:



686; Silva *et al.* 2007: 90; Westerkamp *et al.* 2007: 281; Carvalho & Oliveira 2010: 48; Gonzalez *et al.* 2012: 2929; Moure *et al.* 2012; Rasmussen 2012: 21; Ferrari & Silveira 2015: 266; Luz *et al.* 2016: 522; Lima & Silvestre 2017: 11; Ascher & Pickering 2018.

*Colletes catulus* Vachal, 1904: 26; Friese 1910: 649, 1912: 367; Schrottky 1913: 236; Rasmussen 2012: 21. Synonymy proposed by Moure (1949: 437).

Holotype ♂ examined. (MNHP).

*Colletes inflatus* Vachal, 1909: 49; Cockerell 1913: 185; Rasmussen 2012: 31. Synonymy proposed by Moure (1949: 437).

Lectotype ♀ examined. (MNHP). [hereby designated]

*Colletes speculiventris* Cockerell, 1917a: 438. Synonymy proposed by Moure (1949: 437).

Lectotype ♂ lost. Designated by Moure & Urban (2002: 17). (USNM).

**Diagnosis:** The female of *C. petropolitanus* can be easily recognized by ventral surface of mesosoma completely obscured by remarkably dense pubescence, and posterior hind tibial spur pectinate. The male can be diagnosed through the combination of clypeal mid-longitudinal area not depressed, and malar area very short (~0.4x as long as basal depth of mandible). *Colletes petropolitanus* is most similar to *C. altimontanus*, and in both species the mesosoma is covered with off-white and black hairs intermixed, the tegula is dark-brown and the forewing has a hyaline membrane and dark-brown venation. However, the two species can be differentiated from each other by labrum with mid concavity not margined laterally by longitudinal ridges in *C. petropolitanus* (labral concavity margined laterally by longitudinal ridges in *C. altimontanus*); clypeus without mid-longitudinal depression in *C. petropolitanus* (clypeus with mid-longitudinally depression in *C. altimontanus*); and T2–T5 discs without appressed plumose hairs in *C. petropolitanus* (T2–T5 discs with appressed plumose hairs in *C. altimontanus*).

**Redescription:** FEMALE (Figs. 36A, 36C, 36E):

*Dimensions (mm):* Approximate body length 8.2–9.0; head width 2.6–2.9; head length 2.2–2.4; intertegular distance 2.2–2.6; forewing length 6.2–6.6.

*Colouration:* Black except distal half of mandible and tarsal claws reddish-brown. Wing venation (except proximal veins of forewing dark-brown), stigma, tibial spurs pale-brown.

Tegula, anterior surface of front and mid tibiae, dorsal surface of tarsi (except distal mediotarsi

and distitarsi pale-brown), marginal zones of T1–T5, ventrally reflexed lateral area of T1, S6 (except pale-brown posteromedially) dark-brown. Proximal half of tarsal claws, marginal zones of metasomal sterna pale-yellow.

*Structure:* Labrum medially concave; concavity not margined laterally by longitudinal ridges. Clypeal mid-longitudinal area not depressed. Malar area  $\sim 0.4x$  as long as basal depth of mandible (21:57). Hypostomal carina short and flat. F1  $\sim 1.3x$  as long as its apical width (27:26). UID:LID (52:48). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum pointed. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum  $\sim 0.8x$  as long as metanotum (30:36); metapostnotal pits well-delimited; posterior transverse carina fairly straight and complete. Posteromedial surface of front coxa with small spine. Posterior hind tibial spur pectinate. Hind basitarsus  $3.4x$  longer than broad (51:15). Outer rami of hind tarsal claws  $\sim 2x$  as long as inner rami (9:5). Marginal zone of T1 flat. Marginal zone of S6 not depressed.

*Pubescence:* Head with pale-yellow, plumose, erect, moderately short hairs (except mandible and clypeal disc and subapical pit with suberect setae); paraocular and genal areas with appressed pubescence near eye; paraocular and frontal areas with pale-yellow and fuscous hairs intermixed; genal (towards proboscidal area) and vertexal areas with long hairs. Mesosoma with plumose, erect, moderately long, off-white and black hairs intermixed (except mesoscutum and scutellum with moderately short hairs); mesoscutum posteriorly and metanotum with nearly only off-white hairs; scutellum with only black hairs; ventral mesosoma with very long, remarkably dense pubescence; upper margin of lateral surface of propodeum with black, very long hairs. Legs with fuscous setae (except trochanters and femora with pale-yellow, plumose, long hairs on ventral surface); tibiae and with suberect, minute setae (except hind tibia with erect, moderately short setae on dorsal and posterior surface); femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; basitarsi with suberect, short setae (except mid and hind basitarsi with erect, long setae on posterior margin). Metasomal terga with fuscous, suberect setae (except T1 with pale-yellow, plumose, erect, long hairs); T2–T6 discs with short setae (except those setae minute on T2–T3); T3–T5 also with erect, moderately short setae laterally; T1–T5 with pale-yellow, plumose, appressed, short hairs on marginal zones.



**Figure 36.** *Colletes petropolitanus* Dalla Torre, 1896. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.

Metasomal sterna with pale-yellow hairs (except S6 with fuscous setae posteriorly); S1 with plumose, erect, moderately long hairs; S2 with erect, short, branched apically only hairs (except posterolateral area with plumose, suberect, moderately long hairs); S3–S5 with suberect, minute setae (those setae moderately long posterolaterally); S2–S5 with a line of branched, moderately short hairs near marginal zones; S6 with erect, short setae (except setae moderately long posteriorly).

*Surface sculpture:* Clypeus coarsely punctate; punctures ill-defined and coalescent; interspaces smooth (except rugulose near lower margin). Supraclypeal area densely and moderately coarsely punctate; interspaces rugulose. Malar area substrigulate. Paraocular area densely and moderately finely punctate (except punctures crowded towards clypeus); interspaces smooth (except rugulose near antennal socket). Frontal area punctures crowded and moderately coarse, interspaces smooth (except rugulose towards antennal socket). Vertexal area densely and finely punctate near lateral ocellus; minutely punctate near eye; interspaces smooth throughout. Mesoscutum and mesepisternum densely and coarsely punctate (except mesoscutum largely impunctate posteromedially); interspaces smooth throughout. Scutellum densely and coarsely punctate anteriorly (interspaces smooth); punctures crowded and moderately coarse posteriorly (interspaces imbricate). Metanotum punctation difficult to discern from coarsely rugose integument. Metepisternum with oblique carinae mid-anteriorly; rugose above, densely and finely punctate below. Lateral surface of propodeum densely and finely punctate anteriorly; punctation difficult to discern from coarsely rugulose integument elsewhere. Vertical surface of metapostnotum imbricate above. Metasomal terga interspaces smooth throughout; T1–T2 largely impunctate; T3–T4 moderately sparsely and minutely punctate; T5 densely and finely punctate. Metasomal sterna interspaces imbricate throughout; S1 impunctate; S2 moderately densely and finely punctate; S3–S4 moderately densely and finely punctate (except punctures sparse mid-longitudinally); S5–S6 densely and moderately finely punctate.

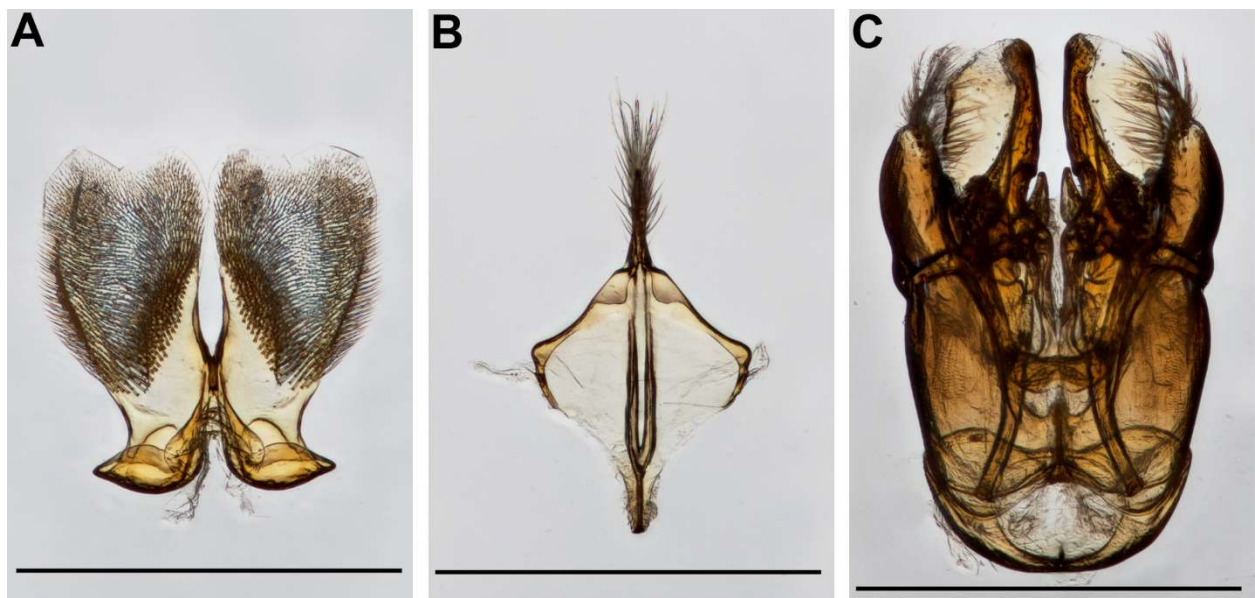
MALE (Figs. 36B, 36D, 36F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 7.2–8.2; head width 2.7–3.0; head length 2.1–2.4; intertegular distance 1.7–2.2; forewing length 6.3–6.8.

*Colouration:* Tibiae entirely black. Mediotarsi pale-brown. S1–S5 posteriorly and S6 entirely dark-brown.

*Structure:* Malar area  $\sim 0.8x$  as long as basal depth of mandible (32:38). F1  $0.8x$  as long as its apical width (24:30). UID:LID (56:45). Horizontal surface of metapostnotum  $\sim 0.7x$  as long as metanotum (26:38). Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 3.3x$  longer than broad (46:14). Outer rami of hind tarsal claws  $\sim 1.7x$  as long as inner rami (10:6). S7, S8 and genital capsule as in Figs. 37A, 37B, 37C, respectively.

*Pubescence:* Clypeus with plumose, moderately long hairs on disc. Paraocular and genal areas with only erect hairs. Hairs of mesoscutum and scutellum as long as those on remaining mesosoma. Mesoscutum with off-white and black hairs intermixed. Ventral mesosoma with sparse pubescence. Legs with pale-yellow setae. Metasomal terga marginal zones with off-white appressed hairs. S6 with pale-yellow, short setae throughout.



**Figure 37.** Dorsal view of the male terminalia of *Colletes petropolitanus*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

*Surface sculpture*: Supraclypeal area with punctures crowded. Paraocular area finely punctate adjacently to inner margin of eye. Mesepisternum moderately sparsely punctate towards ventral surface. Lateral surface of propodeum sparsely and moderately finely punctate posteriorly. T1–T2 finely punctate; T1 sparsely punctate, T2 moderately densely punctate. S3–S4 sparsely punctate mid-longitudinally. S6 finely punctate laterally; moderately coarsely punctate mid-longitudinally.

**Material studied:** *Primary type specimens*: Lectotype ♀ of *C. senilis* – “Type”. “B. M. TYPE; HYM.; 17.a.533”. “B. M. TYPE; HYM.; Colletes; senilis; Smith, 1879”. “PETROPOLIS; Feb. 1857.; J. Gray.”. “Lectotype; 1957; Det. J. S. Moure 1957”. “Colletes; petropolitanus; D.T.; Det. J. S. Moure 1957”. “NHMUK013379537”. {NHMUK}. Holotype ♂ of *C. catulus* – “Tucuman; Rep - Arg”. “Coll. ♂; catulus; Vach.”. “MUSEUM PARIS; Coll. J. VACHAL 1911”. “HOLOTYPE”. “Colletes; catulus; Vach.”. {MNHP}. Lectotype ♀ of *C. inflatus* – “Pérou; Callanga”. “inflatus; ♀ Vach.”. “MUSEUM PARIS; Coll. J. VACHAL 1911”. “LECTOTYPE”. “LECTOTYPE; Colletes inflatus ♀; Vachal, 1909; designated R. Ferrari, 2018”. {MNHP}.

**[hereby designated]**

*Secondary type specimens*: Paralectotypes ♀ and ♂ of *C. senilis* – **BRAZIL – Pará**: prior to 1870, [H. Bates], 1♀1♂, {NHMUK}. Paralectotypes ♀♀ of *C. inflatus* – **BOLIVIA – La Paz**: Mapiri, 1♀, {MNHP}. **PERU – Cusco**: Callanga, 1♀, {MNHP}.

*Additional specimens*: **ARGENTINA – Chaco**: Parque Nacional Chaco, (-26.8875, -59.6223), 20/iv/2008, [A. Taylor], 1♀, {PCYU}. **Corrientes**: Parque Nacional Mburucuya, (-28.0213, -58.0427), 1/i/2010, [N. Veiga], 1♂, {PCYU}; idem, except 12/ii/2010, 1♂. **La Rioja**: La Rioja, i/1923, [M. Gómez], 1♂, {MACN}. **Misiones**: Dos de Mayo, xii/1973, [Fritz], 1♀, {AMNH}. Rio Paraná below Montecarlo, 6/iv/1974, [Vardy & Vardy], 2♀♀, {NHMUK}. **Tucumán**: 3km W Las Juntas, (-26.3997, -65.4986), 20/i/2008, [K. Ramos], 1♂, {RPSP}. Choromoro, 19/i/1996, [J. Sharkey], 1♂, {PCYU}. **BOLIVIA – Santa Cruz**: Sara, 27/xi/1916, [J. Steinbach], 1♀, {MACN}. **BRAZIL – Acre**: Rio Branco, UFAC, 17/viii/1995, [Machado & Santos], 1♂, {RPSP}. **Mato Grosso**: Gallery Forest, (-12.8333, -51.4733), 20/ix/1968, [O. Richards], 1♂, {NHMUK}. **Minas Gerais**: Araxá, 15/iv/1965, [C. Elias], 1♂, {DZUP}; idem, except 22/iv/1965, 1♀; idem, except 28/iv/1965, 1♂; idem, except 5/v/1965, 1♂; idem, except 15/05/1965, 3♂♂; idem, except 20/v/1965, 1♀; idem, except 27/viii/1965, 1♂; idem, except



14/11/1965, 1♂. Belo Horizonte, COPASA/Barreiro, 21/i/1999, [G. Sousa], 1♀, {UFMG}; Estação Ecológica, viii/1998, [D. Yanega], 3♀♀4♂♂, {UFMG}; idem, except 27/v/1998; 1♀. Brasilândia de Minas, Fazenda Brejão, 29/ix/1999, [A. Azevedo], 4♂♂, {UFMG}. Brazópolis, xii/1961, [C. Elias], 5♂♂, {DZUP}. Cássia, Rancho do Popi, 28/iii/1999, [E. Almeida], 9♂♂, {UFMG}. Ibiá, 18/vi/1965, [C. Elias], 2♀♀3♂♂, {DZUP}; idem, except 20/x/1965, [C. Elias], 1♂, {DZUP}. Itajubá, 2/xii/1955, [M. Arié], 1♂, {DZUP}. Mar de Espanha, 4/iii/1911, [J. Zikán], 1♂, {DZUP}. Nova Resende, vii/1961, [C. Elias], 2♂♂, {DZUP}. Paraopeba, Fazenda Itapoá, 22/xii/1998, [V. Silva], 1♂, {UFMG}. Passos, ix/1961, [C. Elias], 1♀, {DZUP}; idem, except 5/xi/1961, 1♂; idem, except 17/iv/1963, 2♂♂; idem, except ix/1963, 1♂; idem, except 1/x/1963, 1♂; idem, except 21/xii/1964, 1♂. Patos de Minas, 20/xi/1965, [C. Elias], 4♂♂, {DZUP}; idem, except 23/xi/1965, 22♀♀24♂♂. Poços de Caldas, (-21.6430, -46.5073), 22/xi/2016, [Ferrari & Freitas], 6♀♀1♂, {PCYU}; idem, except xi/1961, [C. Elias], 2♂♂, {DZUP}. Perdizes, vii/1965, [C. Elias], 1♀, {DZUP}. Ponte Nova, 1/iii/1989, [F. Silveira], 1♀, {MEUV}; idem, except 5/iv/1989, 2♀♀; idem, except 1♀, {UFMG}. Viçosa, unspecified locality, 25/x/1985, [G. Melo], 1♀, {MEUV}; idem, except 31/xii/1985, 1♀; idem, except 15/iii/1986, 1♀; idem, except 25/ii/1989, 1♀; Mata do Paraíso, 22/xi/1989, [M. Thiengo], 2♀♀, {MEUV}; idem, except 1/xii/1989, 2♂♂. **Paraná:** São Mateus do Sul, Fazenda Durgo, 3/iii/2009, [R. Kamke], 1♂, {LUNUFSC}; UN-SIX/Petrobrás, 19/iii/2012, [R. Kamke], 1♀, {LANUFSC}. **Rio de Janeiro:** Rio de Janeiro, xi/1911, [A. Ducke], 1♂, {NHMUK}. **Santa Catarina:** Florianópolis, Praia de Moçambique, 23/xii/2002, [A. Zillikens], 2♂♂, {LANUFSC}. Pomerode, Bairro Testo Alto, 16/xi/2007, [R. Kamke], 1♀, {LANUFSC}; idem, except 4/iv/2008, 1♂. **PARAGUAY – San Pedro:** Cororo, (-23.4527, -56.3964), 8/ii/2007, [E. Willis], 1♀, {PCYU}.

**Range:** ARGENTINA (Chaco, Corrientes, Entre Ríos, La Rioja, Misiones, Tucumán), BOLIVIA (La Paz, Santa Cruz), BRAZIL (Acre, Mato Grosso, Minas Gerais, Pará, Paraná, Rio de Janeiro, Santa Catarina, São Paulo), PARAGUAY (Alto Paraná, San Pedro), PERU (Cusco). See also Fig. 14.

**Biogeographical distribution:** Chocoan dominion (Cerrado and Chocoan provinces), Parana dominion (Atlantic, *Araucaria* and Parana Forests provinces), South American transition zone

(Monte and Puna provinces), and South Brazilian dominion (Madeira, Rondônia and Yungas provinces) at altitudes of 200–3300m a.s.l.

**DNA barcode:** Available. BOLD: AAR9968 (3♀♀1♂). Distance from the nearest neighbour (*C. latitarsis* Robertson, 1891): 5.53–6.43%.

**Floral hosts:** Compositae – *Baccharis dracunculifolia* DC. (this study); *B. spicata* (Lam.) Baill. (Steiner *et al.* 2010). Lamiaceae – *Eriope blanchetii* (Benth.) Harley (Silva *et al.* 2007). Rubiaceae – *Spermacoce* sp. (Ducke 1910b (as *Borreria* sp.)). Sapindaceae – *Matayba guianensis* Aubl. (Carvalho & Oliveira 2010).

**Comments:** Common species that is very widely distributed in South America.

Except for minor differences in pubescence colouration, the type specimens of both *C. catulus* and *C. inflatus* are morphologically indistinguishable from that of *C. senilis* Smith (not Eversmann), and therefore the synonymies originally proposed by Moure (1949), and later acknowledged by many other authors (*e.g.* Moure & Urban 2002; Moure *et al.* 2007, 2012; Ferrari & Silveira 2015; Ascher & Pickering 2018), are endorsed by the present study. Unfortunately, the male lectotype of *C. speculiventris* that was supposedly deposited at the USNM (Moure & Urban 2002; Moure *et al.* 2007, 2012) could not be located neither there (B. Harris, *pers. comm.*), nor at the AMNH (C. Smith, *pers. comm.*), nor at the Illinois Natural History Survey (T. McElrath, *pers. comm.*), and therefore it appears to be lost, at least temporarily. Thus, I am herein also following Moure’s recommendation to treat *C. speculiventris* as a junior synonym of *C. petropolitanus*.

The male holotype of *C. catulus* (NHMUK) is in bad condition—it is missing both antennae, both right wings and the metasoma. However, the diagnostic characters of *C. petropolitanus* found in the head of the male (clypeus without mid-longitudinally depression, and malar area less than half as long as basal depth of mandible) leave no doubt that the former is indeed a junior synonym of the latter.

The type series of *C. inflatus* consists of three female syntypes (not two females and one male as indicated by Vachal in the original description), two of them from Cusco (Peru) and the other from La Paz (Bolivia). When visiting the MNHP in 1986, Moure studied the type series

and labelled one of the females from Cusco as the species' lectotype. However, this designation has never been published and consequently cannot be considered a valid nomenclatural act (ICZN 1999; see Article 9.8). Therefore, I herein formally designate the female from Cusco (the same specimen chosen by Moure) as the lectotype of *C. catulus*. The three specimens are in good condition.

***Colletes rufipes* Smith, 1879**

(Figs. 19, 38, 39, 49B, 50B, 51B, 52B)

*Colletes rufipes* Smith, 1879: 3; Dalla Torre 1896: 44; Schrottky 1901: 211, 1902: 344, 1907: 5, 1913: 236; Dücke 1910a: 80, 1910b: 43; Moure 1942: 295, 1944: 2, 1945: 394; Martins 1994: 232; Zanella 2000: 590; Moure & Urban 2002: 18; Silveira *et al.* 2002: 155; Garófalo *et al.* 2004: 79; Locatelli *et al.* 2004: 158; Bushrow *et al.* 2006: 357; Moure *et al.* 2007: 687; Westerkamp *et al.* 2007: 281; Azevedo *et al.* 2008: 150; Gazola & Garófalo 2009: 611; Hakim & Laroca 2010: 122; Andena *et al.* 2012: 1671; Martins *et al.* 2012: 32; Moure *et al.* 2012; Almeida & Laroca 2013: 57; Ferrari & Silveira 2015: 268; Lima & Silvestre 2017: 11; Ascher & Pickering 2018.

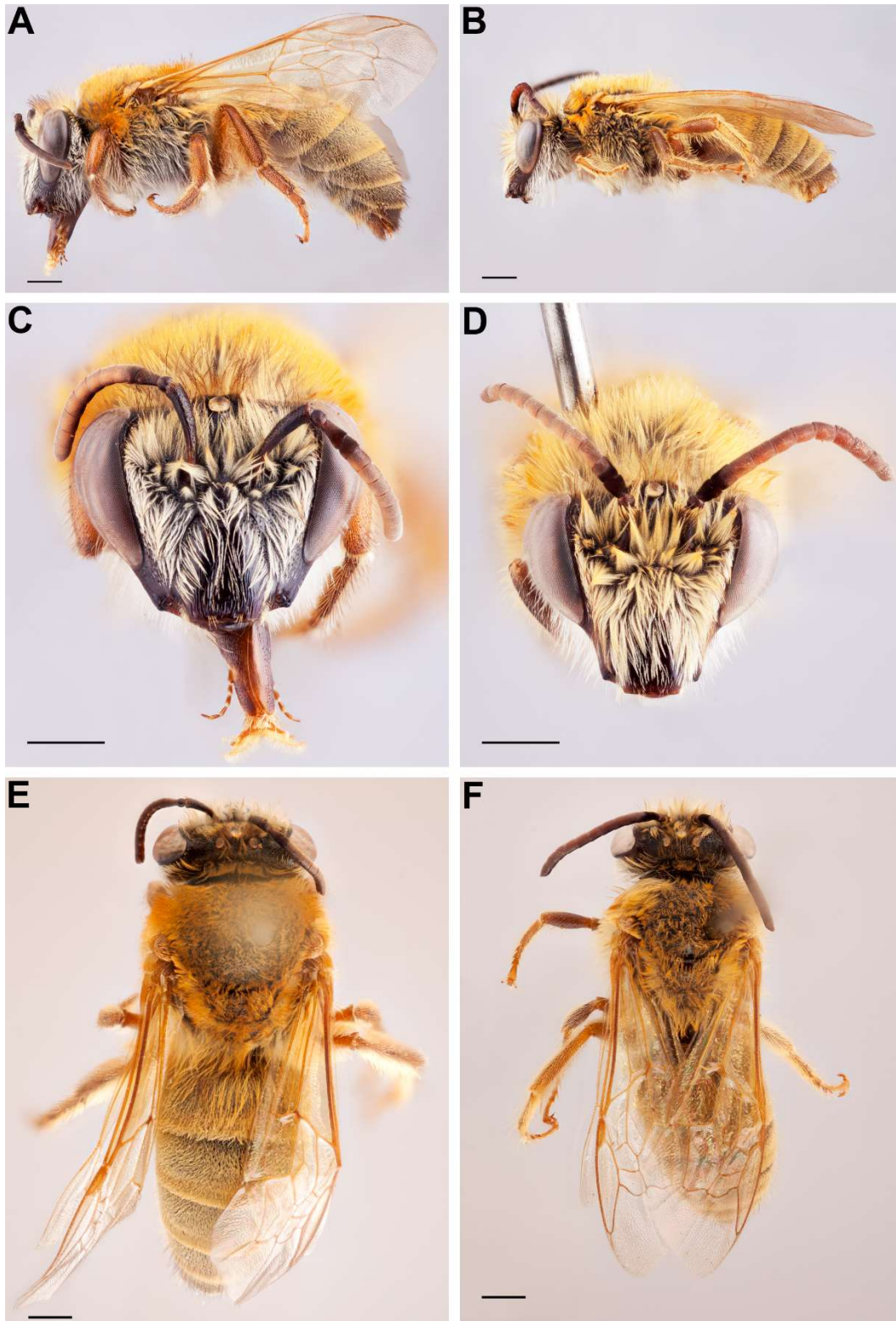
Lectotype ♀ examined. (NHMUK). [hereby designated]

*Colletes rufines* (sic); Silveira & Campos 1995: 377.

**Diagnosis:** *Colletes rufipes* can be diagnosed by the combination of labrum reddish-brown and legs dark-orange. *Colletes rufipes* is most similar to *C. flagellaris* **n. sp.** in that in both the labrum is flat and without ridges, and T2–T5 are covered with pale-yellow, appressed hairs. However, the two species can be distinguished from one other by labrum reddish-brown in *C. rufipes* (labrum black in *C. flagellaris* **n. sp.**); F1 relatively short, 1.4/1.1x (♀/♂) as long as its apical width, in *C. rufipes* (F1 1.9/1.3x (♀/♂) as long as its apical width in *C. flagellaris* **n. sp.**); and legs dark-orange in *C. rufipes* (legs black in *C. flagellaris* **n. sp.**).

**Redescription:** FEMALE (Figs. 38A, 38C, 38E):

*Dimensions (mm):* Approximate body length 9.6–10.5; head width 3.2–3.5; head length 2.6–2.9; intertegular distance 2.4–2.8; forewing length 7.2–7.8.



**Figure 38.** *Colletes rufipes* Smith, 1879. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.

*Colouration:* Black except distal 3/4 of mandible, labrum, distal half of tarsal claws, S6 (except pale-orange mid-longitudinally) reddish-brown. Legs (except front coxa dark-brown), S1 dark-orange. Tegula, wing venation (except vein R of forewing dark-orange), stigma, tibial spurs, marginal zones of T1–T5 and S1–S6 pale-orange. Ventral surface of F3–F10, proximal half of tarsal claws pale-brown. T6, discs of S2–S5 dark-brown.

*Structure:* Labrum medially flat and lacking longitudinal ridges. Clypeal mid-longitudinal area shallowly depressed throughout; depression narrow (0.4x MOD) above, much wider (1.5x MOD) below. Malar area ~1.1x as long as basal depth of mandible (47:43). Hypostomal carina short and flat. F1 ~1.4x as long as its apical width (39:28). UID:LID (66:59). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum modified as a long spine. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by short hairs. Horizontal surface of metapostnotum ~0.7x as long as metanotum (35:51); metapostnotal pits well-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~4.3x longer than broad (78:18). Outer rami of hind tarsal claws ~3x as long as inner rami (16:5). Marginal zone of T1 flat. Marginal zone of S6 depressed.

*Pubescence:* Head with pale-yellow, plumose, erect, moderately long hairs; except mandible with pale-orange setae; clypeus with suberect, moderately short hairs mid-longitudinally; genal area with very long hairs towards proboscis area; frontal and occipital areas with fuscous and pale-yellow hairs intermixed. Mesosoma with pale-orange, plumose, erect, long hairs; except pronotal lobe and mesoscutum with moderately short hairs; lateral surface of propodeum with long hairs on upper margin and short appressed hairs posteriorly. Legs with pale-yellow hairs (except mid and hind tibiae and basitarsi with fuscous and pale-yellow hairs intermixed towards posterior margin); trochanters and femora with plumose, erect, long hairs; femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; tibiae with suberect, short setae (except hind tibiae with erect, moderately long setae); basitarsi with erect, short setae (those hairs long on posterior margin). Metasomal terga with pale-yellow hairs (except T6 with black setae); T1–T5 covered with plumose, dense, appressed hairs; T1 also with plumose, erect, long hairs on disc, those hairs short on T2–T4 laterally; T4–T5 also with black, erect, moderately long setae on discs. Metasomal sterna with pale-yellow

hairs; S1 with plumose, erect, long hairs; those hairs moderately short on S2; S3–S6 with erect, moderately short setae on discs; S3–S5 with a transverse line of plumose, suberect hairs near marginal zones.

*Surface sculpture:* Clypeal mid-longitudinal depression sparsely and moderately finely punctate (interspaces imbricate); adjacent convex area finely striate longitudinally. Malar area moderately densely and finely punctate near lower summit of eye; finely striate elsewhere. Supraclypeal sparsely and moderately coarsely punctate; interspaces imbricate. Paraocular area densely and finely punctate (except moderately coarsely punctate towards clypeus); interspaces smooth throughout. Frontal area punctures crowded and moderately coarse; interspaces rugulose. Vertexal area densely and moderately finely punctate near lateral ocellus; sparsely and finely punctate towards eye; interspaces smooth throughout. Mesoscutum punctures crowded and moderately coarse (except punctures sparser and coarser posteromedially); interspaces smooth. Scutellum densely and coarsely punctate (except sparsely punctate anteriorly and finely punctate posteriorly); interspaces smooth. Metanotum punctures crowded and moderately coarse; punctures limits ill defined. Mesoscutum densely and coarsely punctate, interspaces smooth (except sparsely and moderately finely punctate towards metepisternum posteroventrally, interspaces rugulose). Metepisternum with oblique carinae mid-anteriorly; rugose above; sparsely and moderately finely punctate below (interspaces rugulose). Lateral surface of propodeum sparsely and finely punctate; interspaces rugulose. Vertical surface of metapostnotum rugose above. Metasomal terga with smooth interspaces throughout; T1 moderately sparsely and finely punctate; T2–T5 minutely punctate; T6 densely and finely punctate. Metasomal sterna with imbricate interspaces throughout; S1 minutely punctate; S2–S3 moderately sparsely and finely punctate (except S2 sparsely punctate mid-longitudinally); S4–S5 moderately densely and finely punctate (except densely punctate towards marginal zone); S6 densely and moderately finely punctate (except finely punctate laterally and moderately coarsely punctate posteriorly).

MALE (Figs. 38B, 38D, 38F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 8.2–9.0; head width 2.7–3.1; head length 2.3–2.7; intertegular distance 2.2–2.5; forewing length 6.4–6.9.



*Colouration:* Ventral surface of F2 pale-brown. Ventral surface of front and mid trochanters, dorsal surface of front and mid tibiae dark-brown. Anteroventral surface of mid femur, ventral surface of hind femur pale-yellow. Disc of S6 dark-brown.

*Structure:* Clypeal mid-longitudinal depression very narrow (0.2x MOD) above, much wider (= MOD) below. Malar area ~2.5x as long as basal depth of mandible (62:24). F1 ~1.1x as long as its apical width (33:29). UID:LID (61:50). Horizontal surface of metapostnotum ~0.9x as long as metanotum (35:38). Hind basitarsus ~4.4x longer than broad (57:13). Outer rami of hind tarsal claws ~1.5x as long as inner rami (11:7). Marginal zone of S6 depressed. S7, S8 and genital capsule as in Figs. 39A, 39B, 39C, respectively.

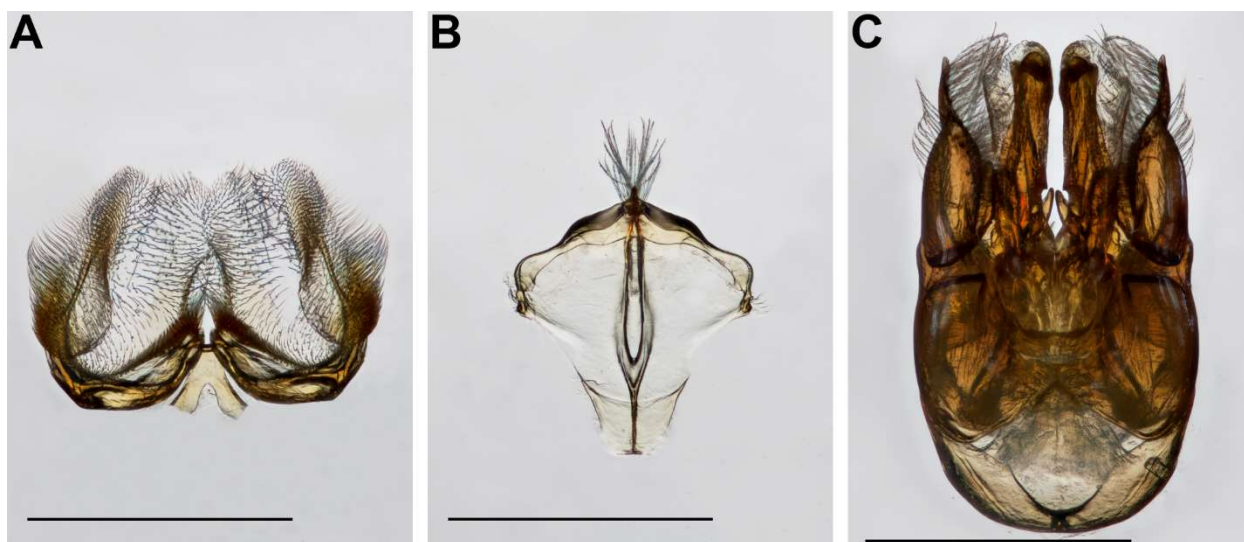
*Pubescence:* Mandible with pale-yellow, plumose hairs. Paraocular area with sparse fuscous hairs near eye. Vertexal area with pale-yellow hairs only. Pronotal and mesoscutal hairs as long as those on scutellum. Lateral surface of propodeum with erect hairs throughout. Mid and hind tibiae and basitarsi with pale-yellow setae only.

*Surface sculpture:* Clypeal mid-longitudinal depression densely punctate; adjacent convex area smooth. Malar area densely and moderately coarsely punctate anteriorly. Supraclypeal and vertexal areas densely punctate throughout. Metanotum moderately densely punctate; punctures limits well defined. Mesepisternum with smooth interspaces throughout. Lateral surface of propodeum densely punctate anteriorly and above. T1–T6 densely and finely punctate. S2 minutely punctate. S3–S5 densely and finely punctate. S6 sparsely punctate on posterior half.

**Material studied:** *Primary type specimen:* Lectotype ♀ – “Type”. “B. M. TYPE; HYM.; 17.a.532”. “Colletes; rufipes Sm.; (Type)”. “Bahia”. “NHMUK013379533”. “LECTOTYPE; Colletes rufipes ♀; Smith, 1879; designated R. Ferrari, 2018”. {NHMUK}. [hereby designated]

*Additional specimens:* **BRAZIL – Ceará:** 18km SE of Assaré, (-6.9755, -39.7750), 3/v/2014, [Almeida, Lucena & Tavares], 1♀, {RPSP}. Serra de Baturité, 28/vi/1908, [A. Ducke], 1♂, {NHMUK}; idem, except 11/vii/1908, 1♀. **Minas Gerais:** Araxá, 5/v/1965, [C. Elias], 2♀♀, {DZUP}; idem, except 19/ix/1965. Belo Horizonte, Parque das Mangabeiras, 13/xi/1996, [J. Damasceno], 1♂, {UFMG}; idem, except 18/xii/1996, 1♂; idem, except 23/i/1997, 1♂; idem, except 31/i/1997, 1♀; idem, except 13/iii/1997, 2♂♂; 10/iv/1997, 1♂; idem, except 2/v/1997, 1♂; idem, except 17/i/1996, [F. Silveira], 1♀. Belo Vale, 25/vii/1986, [G. Melo], 1♂, {MEUV}.

Bonfinópolis de Minas, Fazenda Assa Peixe, (-16.5667, -45.9833), 25/ii/2001, [M. Mazucato], 1♀, {RPSP}. Brumadinho, Parque Estadual da Serra do Rola-Moça, 10/xi/2004, [A. Azevedo], 1♂, {UFMG}. Campos Altos, 28/viii/1965, [C. Elias], 1♀2♂♂, {DZUP}. Catas Altas, Serra do Caraça, 8/i/1999, [F. Silveira], 1♂, {UFMG}; idem, except 28/v/1999, [F. Silveira], 3♂♂, {UFMG}. Conceição do Mato Dentro, 7/ix/2001, [R. Loyola], 1♀, {UFMG}. Coronel Fabriciano, ix/1955, [A. Ferreira], 1♀, {DZUP}. Delfinópolis, iv/1963, [C. Elias], 1♀, {DZUP}. Governador Valadares, 16/ii/1986, [G. Melo], 1♀, {MEUV}. Itueta, 13/vii/1970, [C. Elias], 33♂♂, {DZUP}. Montes Claros, 5/i/1986, [A. Soares], 1♂, {MEUV}. Nova Lima, Parque Estadual da Serra do Rola-Moça, 15/xi/2004, [A. Azevedo], 1♀, {UFMG}. Nova Resende, vii/1961, [C. Elias], 2♀♀5♂♂, {DZUP}. Ouro Preto, locality not indicated, viii/1961, [C. Elias], 1♂, {DZUP}; idem, except 22/vii/1963, [C. Elias], 2♂♂, {DZUP}; Cachoeira Andorinhas, 6/ii/1999, [E. Almeida], 1♀, {UFMG}. Lavras Novas, 5/viii/1995, [Faria, Melo, Daniel, & Paiva], 1♀, {MEUV}. Paraopeba, 28/viii/1987, [F. Silveira], 1♀, {MEUV}; idem, except 31/viii/1987, 1♀, {UFMG}. Passos, iv/1962, [C. Elias], 1♀, {DZUP}; idem, except 1/v/1962, 1♂; idem, except 18/vii/1962, 1♀13♂♂; idem, except 25/vii/1962, 1♂; idem, except 1/viii/1962, 4♂♂; idem, except 8/viii/1962, 1♂; idem, except 22/viii/1962, 1♀1♂; idem, except 1/ix/1962, 1♀; idem, except 27/ix/1962, 1♂; idem, except 24/xii/1962, 1♂; idem, except 5/i/1963, 1♂; idem, except 1/v/1963, 1♂; idem, except 8/vii/1963, 1♂; idem, except 15/vii/1963, 2♂♂; idem, except ix/1963, 1♀; idem, except 9/xii/1963, 1♂. Perdizes, vii/1965, [C. Elias], 6♂♂, {DZUP}. Poços de Caldas, 23/xi/1962, [C. Elias], 1♂, {DZUP}. Pratinha, 4/ix/1965, [C. Elias], 1♀, {DZUP}. Sabará, Chácara do Lessa, 16/vi/2001, [R. Martins], 3♂♂, {UFMG}; Clube Albert Scharlé, 9/i/2000, [F. Silveira], 2♂♂, {UFMG}. Santa Juliana, 4/vi/1965, [C. Elias], 1♀1♂, {DZUP}; idem, except 29/vii/1965, 6♀♀3♂♂. Santana do Riacho, RPPN Brumas do Espinhaço, 6/ii/2005, [A. Azevedo], 1♀, {UFMG}. São Gotardo, 11/vi/1965, [C. Elias], 6♂♂, {DZUP}. Tapira, 27/v/1965, [C. Elias], 1♀1♂, {DZUP}. Uberaba, 13/viii/1965, [C. Elias], 16♀♀7♂♂, {DZUP}. Viçosa, 23/xii/1985, [G. Melo], 1♀, {MEUV}. **Rio Grande do Sul:** Pelotas, 7/iv/1964, [C. Biezanko], 1♀, {NHMKU}. **São Paulo:** Cajuru, Fazenda Santa Carlota, 28/xii/1986, [Camargo], 1♀1♂, {PCYU}; idem, except 21/xi/1988, [Garófalo, Camillo & Serrano], 1♂. Pedregulhos, Reserva Ecológica, 13/i/1992, [Garófalo, Camillo & Serrano], 1♂, {PCYU}; idem, except 16/i/1992, 1♀; idem, except 17/i/1992, 1♀. Rio Claro, Chácara Paraízo, v/1939, [Claretiano], 1♂, {SEMC}.



**Figure 39.** Dorsal view of the male terminalia of *Colletes rufipes*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Range:** BRAZIL (Bahia, Ceará, Minas Gerais, Rio Grande do Sul, São Paulo). See also Fig. 19.

**Biogeographical distribution:** Chacoan dominion (Caatinga and Cerrado provinces), Parana dominion (Parana Forest province) at altitudes of 100–1400m a.s.l.

**DNA barcode:** Available. BOLD: ADG1971 (1♂). Distance from the nearest neighbour (*C. meridionalis*): 10.55–11.51%.

**Floral hosts:** Compositae – *Sphagneticola trilobata* (L.) Pruski (Locatelli *et al.* 2004 (as *Complaya trilobata* (L.) Stroher)), *Vernonia* sp. (Schrottky 1901, 1907). Erythroxylaceae – *Erythroxylum suberosum* A. St.-Hil. (Andena *et al.* 2012). Sapindaceae – *Sapindus* sp. (Ducke 1910b), *Serjania* sp. (Ducke 1910b), *Spermacoce* sp. (Ducke 1910b (as *Borreria* sp.)), *Talisia angustifolia* Radlk. (Andena *et al.* 2012).

**Comments:** Common species widely distributed in Brazil.

As Smith did not designate a name-bearing type in his original description of *C. rufipes*, coupled with the fact that is impossible to know whether the description was based on a single

specimen or not, the female that is deposited at the NHMUK is a syntype (ICZN 1999; see Recommendation 73F). This specimen, which is in good condition, is herein designated as the species' lectotype.

***Colletes rugicollis* Friese, 1900**

(Figs. 24, 40, 41, 47B, 47D, 53B)

*Colletes rugicollis* Friese, 1900: 183; Schrottky 1902: 347, 1907: 19, 1913: 237; Vachal 1904: 26; Friese 1908: 11, 1916: 290, 1921: 75; Ducke 1912: 78; Moure 1944: 2, 1949: 438; Michener 1954: 17; Michener *et al.* 1958a: 4, 1958b: 208; Sakagami & Laroca 1971: 219; Moure & Urban 2002: 19; Silveira *et al.* 2002: 155; Moure *et al.* 2007: 687; Azevedo *et al.* 2008: 150; Rasmussen & Ascher 2008: 94; Hakim & Laroca 2010: 122; Steiner *et al.* 2010: 23; Gonçalves *et al.* 2012: 55; Moure *et al.* 2012; Ferrari & Silveira 2015: 270; Ramos *et al.* 2015: 338; Ascher & Pickering 2018.

Lectotype ♀ examined. Designated by Moure & Urban (2002: 19). (ZMB).

*Colletes punctatissimus* Schrottky, 1902: 347; Silveira & Campos 1995: 377. Synonymy proposed by Moure (1944: 2).

Holotype ♀ lost. (MZSP).

**Diagnosis:** Both sexes of *C. rugicollis* can be diagnosed through the combination of hypostomal carina produced as a tall concave lamella in profile, and T1 with a convex marginal zone.

*Colletes rugicollis* is most similar to *C. argentinus*, since in both the vertexal area has a protrusion below lateral ocellus, and T1 is coarsely and densely punctate and its marginal zone is convex. However, *C. rugicollis* can be differentiated from *C. argentinus* by hypostomal carina produced as a tall, concave lamella (hypostomal carina short and flat in *C. argentinus*); and paraocular area with mostly pale-yellow hairs (paraocular area with mostly off-white hairs in *C. argentinus*). Their males can also be distinguished by supraclypeal area densely punctate in *C. rugicollis* (supraclypeal area sparsely punctate in *C. argentinus*).



**Figure 40.** *Colletes rugicollis* Friese, 1900. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.

**Redescription:** FEMALE (Figs. 39A, 39C, 39E):

*Dimensions (mm):* Approximate body length 9.3–10.7; head width 3.1–3.4; head length 2.4–2.8; intertegular distance 2.6–3.2; forewing length 8.0–8.7.

*Colouration:* Black except distal 2/3 of mandible, distal half of tarsal claws reddish-brown. Ventral surface of F3–F10, wing venation (except veins R, M+Cu and V of forewing black), stigma, hind tarsus (except distitarsus pale-brown), marginal zones of T1–T5, ventrally reflexed lateral areas of T2, S2–S6 (except pale-brown mid-longitudinally) dark-brown. Tibial spurs, proximal half of tarsal claws, ventrally reflexed lateral areas of T1 pale-brown. Marginal zones of metasomal sterna pale-yellow.

*Structure:* Labrum medially concave; concavity not margined laterally by longitudinal ridges. Clypeus without mid-longitudinal depression. Malar area  $\sim 0.35\times$  as long as basal depth of mandible (16:48). Hypostomal carina produced as a tall, concave lamella in profile. F1  $\sim 1.3\times$  as long as its apical width (36:30). UID:LID (61:57). Frontal area with a protrusion below lateral ocellus. Vertexal area flat behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum pointed. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum  $0.75\times$  as long as metanotum (30:40); metapostnotal pits poorly-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus  $\sim 2.8\times$  longer than broad (54:19). Outer rami of hind tarsal claws  $\sim 1.75\times$  as long as inner rami (14:8). Marginal zone of T1 convex. Marginal zone of S6 depressed.

*Pubescence:* Head with pale-yellow, plumose, erect, moderately short hairs (except mandible with suberect setae); clypeus with short hairs; paraocular, interantennal and frontal areas also with sparse, moderately long hairs; vertexal and genal areas with black, plumose, erect, long hairs (except short behind upper summit of eye). Mesosoma with black, plumose, erect, long hairs; mesoscutum with moderately short, off-white and black hairs intermixed; lateral surface of propodeum with off-white, short hairs. Legs with black hairs; trochanters and femora with plumose, erect, very long hairs; femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; tibiae and basitarsi with erect, moderately short setae (except moderately long on posterior margin of mid basitarsus and posterior surface of hind tibia; long on posterior margin of hind basitarsus). Metasoma covered with black hairs throughout; T1 with plumose, erect, long hairs; T2–T5 with erect, minute setae (except moderately long



laterally); T6 with suberect, moderately short setae; S1 with plumose, erect, moderately long hairs; S2 with erect, moderately long setae and short plumose hairs intermixed; S3–S6 with suberect, short setae (longer on S3, shorter on S6); S3–S5 with a line of plumose, short hairs near marginal zones.

*Surface sculpture:* Clypeus densely and coarsely punctate mid-longitudinally (interspaces rugulose); punctures crowded and moderately coarse elsewhere (interspaces smooth). Supraclypeal area with sparse moderately coarse punctures; interspaces rugulose. Malar area substrigulate. Paraocular area punctures crowded and moderately coarse (except punctures fine near antennal socket); interspaces smooth throughout. Frontal area punctures crowded and coarse; interspaces smooth. Vertexal area densely and moderately finely punctate near lateral ocellus; fine and minute punctures intermingled towards eye; interspaces smooth throughout. Mesoscutum and mesepisternum with punctures crowded and very coarse (except mesoscutum only densely punctate posteromedially); interspaces smooth throughout. Scutellum densely and coarsely punctate (except punctures moderately dense anteriorly and crowded towards posterior margin); interspaces smooth throughout. Metanotum rugose. Metepisternum with oblique carinae mid-anteriorly; rugose elsewhere. Lateral surface of propodeum densely and moderately coarsely punctate; interspaces rugulose. Vertical surface of metapostnotum rugose above. T1–T2 densely punctate (except punctures sparse mid-longitudinally); T1 coarsely punctate; T2 moderately finely punctate; interspaces smooth throughout. T2–T5 finely and moderately sparsely punctate; interspaces smooth. Metasomal sterna with imbricate interspaces. S2–S4 densely and moderately finely punctate. S5 punctures crowded and fine. S6 densely and finely punctate (except moderately densely punctate mid-longitudinally).

MALE (Figs. 40B, 40D, 40F). As in female, except for usual secondary sexual characteristics and as follows:

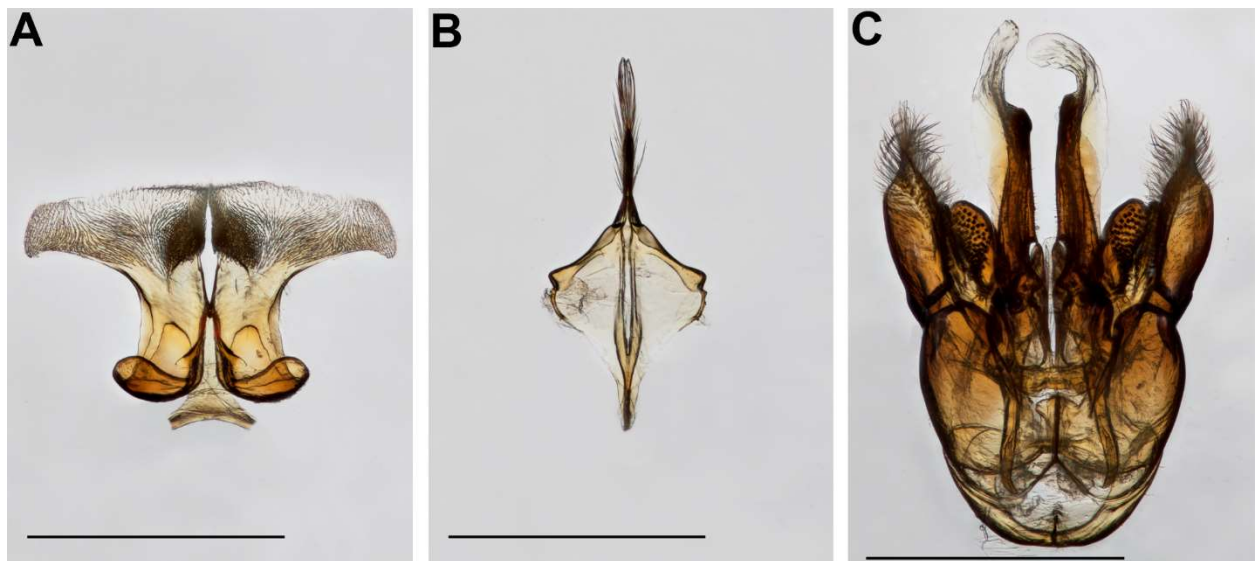
*Dimensions (mm):* Approximate body length 7.1–8.0; head width 2.8–3.1; head length 2.2–2.4; intertegular distance 2.1–2.4; forewing length 6.8–7.1.

*Colouration:* Ventral surface of F2, dorsal surface of mid and hind tibiae dark-brown. Tibial spurs pale-yellow. Dorsal surface of mid and hind tarsi pale-brown (except basitarsi dark-brown). Ventrally reflexed lateral areas of T1 reddish-brown.

*Structure:* Malar area  $\sim 0.5\times$  as long as basal depth of mandible (18:38). F1 as long as its apical width (30:30). UID:LID (55:44). Horizontal surface of metapostnotum  $0.75\times$  as long as metanotum (25:41); metapostnotal pits well-delimited. Hind basitarsus  $\sim 3.8\times$  longer than broad (49:13). Outer rami of hind tarsal claws  $1.8\times$  as long as inner rami (18:10). Marginal zone of S6 not depressed. S7, S8 and genital capsule as in Figs. 41A, 41B, 41C, respectively.

*Pubescence:* Mesoscutum with mostly off-white hairs. Lateral surface of propodeum with black, erect, long hairs. T1 with short hairs. S2 covered with short setae only.

*Surface sculpture:* Clypeus evenly densely and coarsely punctate; interspaces smooth throughout. Supraclypeal area densely punctate. T1 very coarsely punctate. T2 evenly densely and moderately coarsely punctate. T3–T5 moderately finely punctate. Metasomal sterna with smooth interspaces. S6 sparsely and minutely punctate.



**Figure 41.** Dorsal view of the male terminalia of *Colletes rugicollis*. (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**Material studied:** *Primary type specimen:* Lectotype ♀ – “Bolivia; Yungas; 98”. “*Colletes* ♀; *rugicollis*; det. Friese 1898”. “Coll.; Friese”. “SYNTYPE; *Colletes*; *rugicollis* Fr.; Examined C Rasmussen’ 07”. “LECTOTYPE; *Colletes rugicollis*; Friese, 1900; lab. Melo, 2015”.

“<http://coll.mfn-berlin.de/u/; 58f9bd>”. {ZMB}.

*Additional specimens:* **BOLIVIA – La Paz:** Chulumani, R. Portugais Finca, (-16.3666, -67.5000), 30/iv/1997, [L. Masner], 1♀, {PCYU}. Coroico, El Bagante, 18/iv/1997, [L. Masner], 1♂, {CNC}. **BRAZIL – Minas Gerais:** Araxá, 17/ii/1965, [C. Elias], 1♂, {DZUP}. Baependi, Parque Estadual da Serra do Papagaio, 9/iv/2008, [F. Silveira], 1♀2♂♂, {UFMG}. Belo Horizonte, COPASA/Barreiro, 29/iv/1999, [J. Moreira], 1♀, {UFMG}; Parque das Mangabeiras, 7/vi/1997, [R. Carmo], 2♀♀, {UFMG}; idem, except 24/iv/1997, 1♀; idem, except 13/ii/1997, [J. Damasceno], 1♂. Catas Altas, Serra do Caraça, xi/1961, [Martins & Silva], 3♀♀3♂♂, {MZSP}. Lambari, Serra da Campanha, (-21.9577, -45.3616), 27/xii/2001, 2♂♂, [F. Silveira], {UFMG}. Viçosa, 16/xii/1986, [G. Melo], 1♀1♂, {MEUV}; idem, except 29/iii/1987, [Melo & Soares], 1♀; 1/xii/1989, [M. Thiengo], 1♀. **Paraná:** Near Guaratuba, Estrada dos Castelhanos, 4/v/2003, [Melo & Aguiar], 1♀, {RPSP}. Piraquara, 29/iii/2007, [G. Melo], 1♀, {RPSP}; idem, except 23/i/2003, [A. Aguiar], 1♂. São Mateus do Sul, UN-SIX/Petrobrás, 21/i/2011, [R. Kamke], 1♀, {LANUFSC}; Fazenda Durgo, 3/iii/2009, [R. Kamke], 1♂, {LANUFSC}. **Rio de Janeiro:** Parque Nacional do Itatiaia, 28/xii/1947, [J. Zikán], 1♀, {INPA}; idem, except 16/iii/2007; [A. Azevedo], 1♀, {UFMG}. **Santa Catarina:** Pomerode, Testo Alto, 18/xi/2007, [R. Kamke], 1♂, {LANUFSC}; idem, except 21/iii/2008, 1♀. São Martinho, 12/iii/2007, [L. Rocha], 1♂, {LANUFSC}. **PERU – San Martín:** Naciente del Río Negro spring, (-6.0850, -77.2710), 17/v/2015, [C. Rasmussen], 1♂, {PCYU}.

**Range:** BOLIVIA (La Paz), BRAZIL (Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina, São Paulo), PERU (San Martín). See also Fig. 24.

**Biogeographical distribution:** Chocoan dominion (Cerrado province), Parana dominion (*Araucaria* Forest, Atlantic and Parana Forest provinces), South American transition zone (Puna Province), and South Brazilian dominion (Ucayali province) at altitudes of 600–2500m a.s.l.

**DNA barcode:** Available. BOLD: ACV1586 (1♀ and 2♂♂). Distance from the nearest neighbour (*C. argentinus*): 2.89–4.03%.

**Floral hosts:** Compositae – *Mikania cordifolia* (L.f) Wild. (this study), *Solidago chilensis* Meyen (this study). Lamiaceae – *Hyptis* sp. (this study). Solanaceae – *Physalis* sp. (Friese 1921), *Solanum* sp. (Steiner *et al.* 2010).

**Comments:** Relatively common species that is widely distributed in South America.

Regrettably, the holotype of *C. punctatissimus* that was supposedly deposited at the MZSP (Moure & Urban 2002; Moure *et al.* 2007, 2012) is currently lost (Rasmussen *et al.* 2009; Ferrari & Silveira 2015; Ramos *et al.* 2015). According to Moure (1944), who originally synonymized *C. punctatissimus* with *C. rugicollis*, the holotype is a male not a female as indicated by Schrottky (1902: 347) in the original description of the species.

***Colletes sertanicola* Ferrari, new species**

(Figs. 12, 42, 43, 55B)

**Diagnosis:** *Colletes sertanicola* **n. sp.** can be readily diagnosed by the combination of F1 relatively long, 1.3/1.1x (♀/♂) as long as its apical width, and T1–T2 pale-brown (except T1–T2 dark-brown anteriorly in the male). The male of *Colletes sertanicola* **n. sp.** is most similar to that of *C. chicoi* **n. sp.** (the female of the latter is unknown) as both possess pale legs and brownish T1–T2. However, they can be distinguished from each other by the comparatively longer F1, 1.1x as long as its apical width, in *C. sertanicola* **n. sp.** (F1 0.8x as long as its apical width in *C. chicoi* **n. sp.**); mesoscutum sparsely punctate anteriorly in *C. sertanicola* **n. sp.** (mesoscutum densely punctate anteriorly in *C. chicoi* **n. sp.**); T1 dark-brown anteriorly in *C. sertanicola* **n. sp.** (T1 pale-brown anteriorly in *C. chicoi* **n. sp.**).

**Description:** FEMALE (Figs. 42A, 42C, 42E):

*Dimensions (mm):* Approximate body length 7.5; head width 2.6; head length 2.1; intertegular distance 1.9; forewing length 6.3.

*Colouration:* Black except legs (except front and mid trochanters and front femur dark-brown dorso-posteriorly, distitarsi pale-yellow dorsally), wing venation (except vein R of forewing dark-brown), metasoma (marginal zones of terga and S6 laterally marked with dark-brown) pale-brown. Mandible (except distal 1/3 reddish-brown), distal half of tarsal claws dark-

orange. Ventral surface of F2–F10 dark-brown. Tegula, stigma (except margins dark-brown), tibial spurs, proximal half of tarsal claws pale-yellow.

*Structure:* Labrum medially convex; convexity margined laterally by longitudinal ridges. Clypeal mid-longitudinal area deeply and moderately narrowly (0.6x MOD) depressed on upper 2/3; depression much shallower and broader (maximum width 1.5x MOD) below. Malar area ~1.3x as long as basal depth of mandible (38:29). Hypostomal carina short and flat. F1 ~1.3x as long as its apical width (31:24). UID:LID (50:44). Frontal area without protrusion below lateral ocellus. Vertexal area concave near upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum modified as a long spine. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum subequal in length to metanotum (23:24); metapostnotal pits well-delimited; posterior transverse carina straight and incomplete. Posteromedial surface of front coxa with strong spine. Posterior hind tibial spur ciliate. Hind basitarsus ~3.6x longer than broad (51:14). Outer rami of hind tarsal claws 2.5x as long as inner rami (10:4). Marginal zone of T1 flat. Marginal zone of S6 depressed.

*Pubescence:* Head with off-white, plumose, erect, moderately long hairs; except clypeal mid-longitudinal depression and lateral slopes and paraocular area (adjacent to outer margin of eye) with suberect hairs; paraocular, interocellar and vertexal areas with off-white and fuscous hairs intermixed. Mesosoma with pale-yellow, plumose, erect, moderately long hairs; except pronotal lobes and mesoscutum with moderately short hairs; scutellum with pale-yellow and fuscous hairs intermixed posteriorly; mesepisternum with off-white, long hairs; lateral surface of propodeum with appressed hairs on disc. Legs with pale-yellow hairs; except trochanters and femora with off-white, plumose, long hairs; femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; front and mid tibiae with suberect, short setae (except posterior surface with erect setae); hind tibia and basitarsi with erect, moderately short setae (except posterior margins of front and mid basitarsi with long setae, hind basitarsus with very long setae). Metasoma terga covered with pale-yellow, appressed, plumose, short hairs; except T6 black, erect, moderately long setae; T1 with erect, plumose, long hairs; T4–T5 with black, erect, moderately short setae on discs (those setae pale-yellow and longer laterally). Metasoma sterna with pale-yellow hairs throughout; S1 with plumose, erect, moderately long hairs; S2 with erect, moderately short, branched only apically hairs; S3–S6 discs covered with erect, short setae

(except S4–S5 with moderately long setae adjacently to marginal zones; S1–S5 marginal zones with a line of plumose, suberect, moderately short hairs.

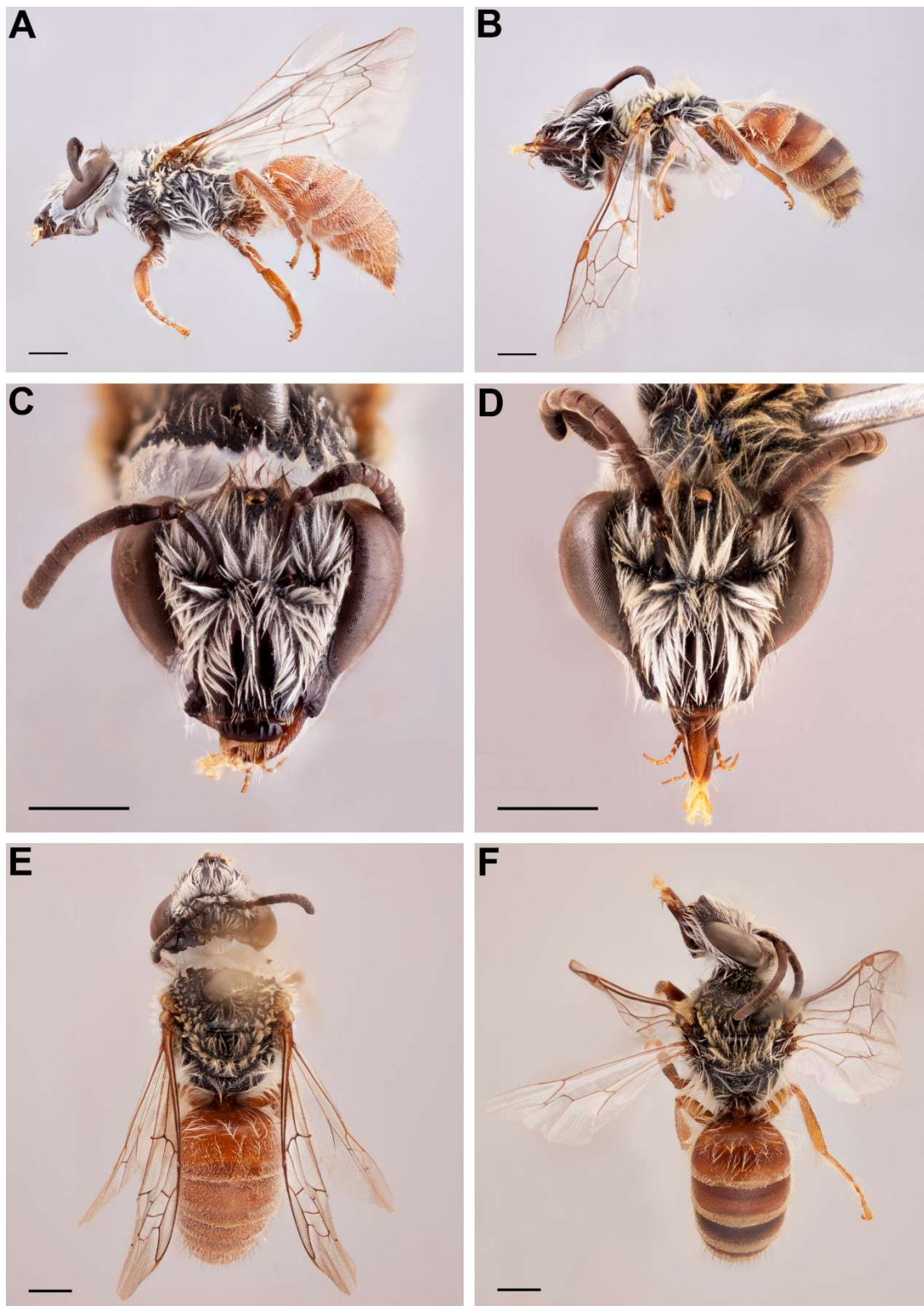
*Surface sculpture:* Clypeal mid-longitudinal depression densely and finely punctate; adjacent convex area smooth (except lower transverse band finely longitudinally striate). Supraclypeal area sparsely and finely punctate; interspaces imbricate. Malar area sparsely and moderately finely punctate; punctures ill-defined and coalescent towards eye; interspaces smooth (except imbricate near mandible). Paraocular area densely and moderately finely punctate (except juxtantennal area sparsely punctate); interspaces smooth below, imbricate above. Frontal area densely and moderately coarsely punctate; interspaces rugulose. Vertexal area densely punctate anteriorly, more sparsely punctate towards occipital area; punctures minute near eye, punctures coarser near lateral ocellus; interspaces smooth throughout. Mesoscutum coarsely punctate; punctures moderately dense anterolaterally and sparse posteromedially; interspaces smooth throughout. Scutellum moderately densely and coarsely punctate (except punctures sparse mid-longitudinally); interspaces smooth. Metanotum moderately densely and moderately coarsely punctate; interspaces imbricate. Mesepisternum sparsely and coarsely punctate (except densely punctate anterior to episternal groove and below scrobe); interspaces smooth (except imbricate anterior to episternal groove). Metepisternum finely and obliquely striate anteriorly; sparsely and moderately finely punctate above and below (interspaces imbricate). Lateral surface of propodeum sparsely and moderately finely punctate; interspaces rugulose. Vertical surface of metapostnotum imbricate above. Metasomal terga with smooth interspaces throughout; T1 sparsely and finely punctate; T2–T6 minutely punctate. Metasomal sterna with imbricate interspaces throughout; S1 minutely punctate; S2–S5 moderately densely and finely punctate (except punctures sparse mid-longitudinally); S6 densely and moderately finely punctate posterolaterally, impunctate elsewhere.

MALE (Figs. 42B, 42D, 42F). As in female, except for usual secondary sexual characteristics and as follows:

*Dimensions (mm):* Approximate body length 6.3; head width 2.4; head length 1.9; intertegular distance 1.7; forewing length 5.8.

*Colouration:* Front and mid femora, dorsal surface of tibiae dark-brown. Dorsal surface of tarsi pale-yellow. T1–T2 anteriorly dark-brown. T3–T6 discs black.





**Figure 42.** *Colletes sertanicola* n. sp. Female: (A) habitus, lateral view; (C) face, frontal view; (E) habitus, dorsal view. Male: (B) habitus, lateral view; (D) face, frontal view; (F) habitus, dorsal view. Scale bars = 1mm.

*Structure:* Clypeal mid-longitudinal area deeply and narrowly (0.4x MOD) depressed above; depression progressively shallower and broader (maximum width 1.3x MOD) towards lower margin. Malar area ~1.7x as long as basal depth of mandible (42:24). F1 ~1.1x as long as its apical width (27:24). UID:LID (61:48). Dorsolateral angle of pronotum pointed. Horizontal surface of metapostnotum subequal in length to metanotum (23:24); metapostnotal pits well-delimited; posterior transverse carina sinuous. Posteromedial surface of front coxa with weak spine. Hind basitarsus 4.4x longer than broad (44:11). Outer rami of hind tarsal claws 2.5x as long as inner rami (14:10). Marginal zone of S6 depressed. S7, S8 and genital capsule as in Figs. 43A, 43B, 43C, respectively.

*Pubescence:* Head with pale-yellow hairs (except paraocular, interocellar and vertexal areas with fuscous and pale-yellow hairs intermixed). Scutellum with pale-yellow hairs throughout. Lateral surface of propodeum with long, erect hairs. Appressed hairs on metasomal terga restricted to marginal zones. T6 covered with pale-yellow setae. S2 with plumose hairs. S5–S6 with moderately long setae on discs.

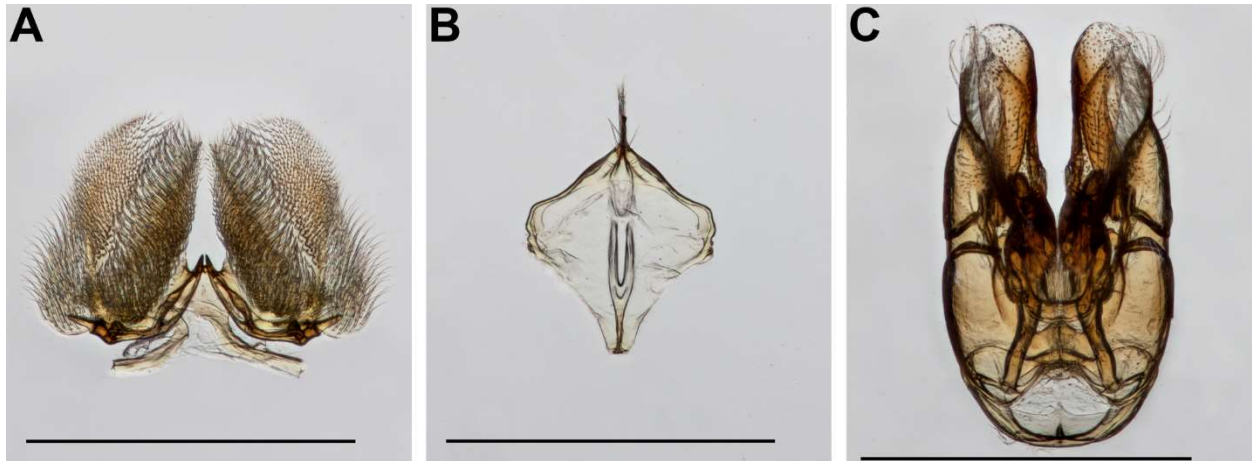
*Surface sculpture:* Supraclypeal area with rugulose interspaces. Frontal area punctures crowded. Vertexal area densely punctate throughout. Scutellum sparsely punctate. Metepisternum with rugulose interspaces above. Vertical surface of metapostnotum rugulose above. T1 moderately densely punctate; moderately fine and minute punctures intermingled throughout; T2–T4 densely and moderately finely punctate (T2 with imbricate interspaces anteriorly); T5 punctures ill-defined and difficult to discern from rugulose interspaces. S2–S6 sparsely and finely punctate.

**Type material:** *Holotype* ♀ – “Monte Santo, BA; Col. 20/i/2000; Emg 8/iv/2000; N: b24 Aprisco”. “Colletes sp; DET. Zanella 2002”. “412”. “MZUEFS; #27148”. “CCDC-30383 C06”. “HOLOTYPE; Colletes sertanicola ♀; Ferrari, new species”. {MZUEFS}.

*Paratypes:* **BRAZIL – Bahia:** Monte Santo, 13/i/2000, 1♂, {MZUEFS}.

**Range:** BRAZIL (Bahia). See also Fig. 12.

**Biogeographical distribution:** Chacoan dominion (Cerrado province) at altitudes of 300–600m a.s.l.



**Figure 43.** Dorsal view of the male terminalia of *Colletes sertanicola* **n. sp.** (A) S7; (B) S8; (C) genital capsule. Scale bars = 1mm.

**DNA barcode:** Unavailable.

**Floral hosts:** Unknown.

**Etymology:** This species is named after the “sertão nordestino”, an important region in the Brazilian northeast where the type locality is located.

**Comments:** Seemingly a rare species which is only known to me by two specimens.

Part of the holotype’s head (specially the genal and occipital areas) as well as its pronotum and anterior mesoscutal area are covered with white glue. Otherwise the specimen is in good condition.

### ***Colletes sexangulus* Ferrari, new species**

(Figs. 33, 44)

**Diagnosis:** The female *C. sexangulus* **n. sp.** (the male is unknown) can be diagnosed by the combination of labrum medially concave and margined laterally by longitudinal ridges, clypeal convex area obliquely striate, and mesoscutum covered with pale-orange hairs. *Colletes sexangulus* **n. sp.** is most similar to *C. furfuraceus* as in both the labrum is concave mid-

longitudinally and concavity is marginal by lateral ridges, the mesoscutum is covered with pale-orange pubescence and the metasomal terga (except T6) with pale-yellow appressed hairs. However, these species can be differentiated by clypeus deeply and broadly (maximum breadth 1.8x MOD below) depressed mid-longitudinally in *C. sexangulus* **n. sp.** (clypeus not depressed in *C. furfuraceus*); hind basitarsus relatively long, ~4x MOD, in *C. sexangulus* **n. sp.** (hind basitarsus ~3.5x MOD in *C. furfuraceus*); and T1–T5 with pale-yellow marginal zones in *C. sexangulus* **n. sp.** (T1–T5 marginal zones dark-brown in *C. furfuraceus*).

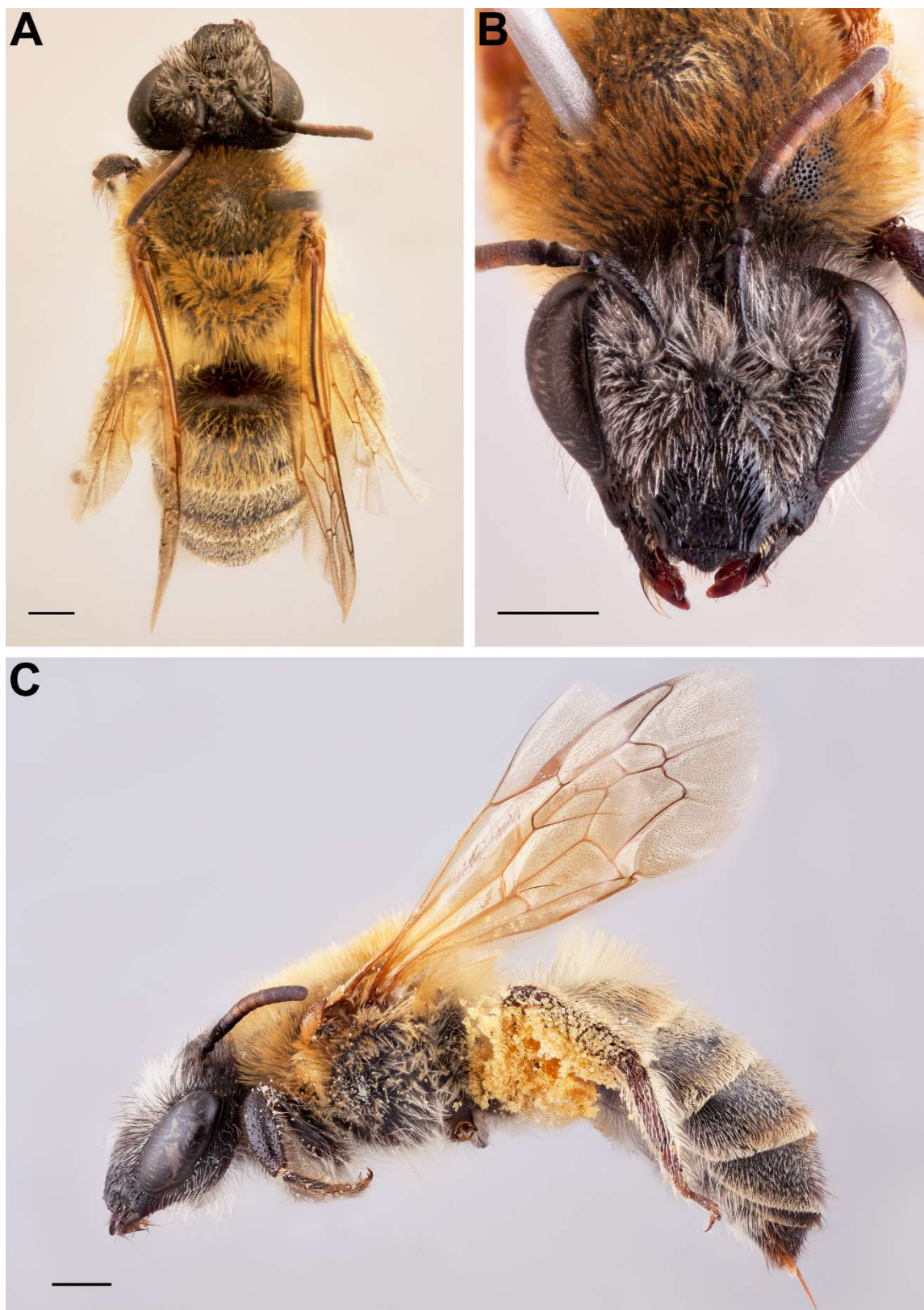
**Description:** FEMALE (Figs. 44A–C):

*Dimensions (mm):* Approximate body length 9.8; head width 3.4; head length 2.7; intertegular distance 2.8; forewing length 7.9.

*Colouration:* Black except distal half on mandible, distal 3/5 of tarsal claws, S6 mid-longitudinally reddish-brown. Ventral surface of flagellum (except ventral surface of F2–F5 pale-brown), dorsal surface of distitarsi and hind tibia and basitarsus, S2 posteromedially, S3–S5 posteriorly dark-brown. Tegula, wing venation (except forewing veins R1, RS, 2r-m and 2m-cu of dark-brown and R black), stigma pale-orange. Tibial spurs, marginal zones of T1–T5 and S1–S6 pale-yellow. Proximal 2/5 of tarsal claws pale-brown.

*Structure:* Labrum medially concave; concavity margined laterally by longitudinal ridges. Clypeal mid-longitudinal area deeply and narrowly (0.6x) depressed above; depression slightly shallower and much broader (maximum width 1.8x MOD) below. Malar area 0.8x as long as basal depth of mandible (40:48). Hypostomal carina short and flat. F1 ~1.4x as long as its apical width (29:21). UID:LID (67:59). Frontal area without protrusion below lateral ocellus. Vertexal area concave behind upper summit of eye in postero-lateral view. Dorsolateral angle of pronotum pointed. Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed hairs. Horizontal surface of metapostnotum ~0.5x as long as metanotum (27:50); metapostnotal pits well-delimited; posterior transverse carina sinuous and complete. Posteromedial surface of front coxa without spine. Posterior hind tibial spur ciliate. Hind basitarsus ~4.1x longer than broad (58:14). Outer rami of hind tarsal claws 2x as long as inner rami (18:9). Marginal zone of T1 flat. Marginal zone of S6 depressed.





**Figure 44.** *Colletes sexangulus* n. sp. Female: (A) habitus, dorsal view (B); face, frontal view; (C) habitus, lateral view. Scale bars = 1mm.

*Pubescence:* Head with off-white, plumose, erect, moderately long hairs; except mandible with fuscous setae; interantennal area with long hairs; paraocular and frontal areas with off-white and black hairs intermixed; vertexal area with black, long hairs; genal area with moderately short hairs above. Mesosoma with pale-orange, plumose, erect, moderately long hairs; those hairs longer on metanotum, longest on upper margin of lateral surface of propodeum; mesepisternum and metepisternum with pale-yellow, long hairs; disc of lateral surface of propodeum with appressed, short hairs. Legs with pale-yellow setae (except front tibia and basitarsus with fuscous setae); trochanters and femora with plumose, erect, long hairs; femoral and tibial scopae with branched apically only, suberect, very long hairs anteriorly; tibiae and basitarsi with erect, moderately long setae (except front tibia with suberect short setae anterodorsally and basitarsi with long setae on posterior margins). Metasomal terga covered with pale-yellow, plumose, appressed, short hairs (except T5–T6 with black, suberect, moderately short setae); T1 also with plumose, erect, very long hairs; T2–T4 also with pale-yellow, erect, short setae (those setae black and longer on T4). Metasomal sterna with pale-yellow hairs (except S6 with fuscous setae posteriorly); S1 with plumose, erect, moderately long hairs; S2–S6 discs with erect, moderately short setae (except S2 with plumose hairs posteromedially and S3 with short setae anteriorly); S2–S4 marginal zones with a transverse line of plumose, suberect hairs.

*Surface sculpture:* Clypeal mid-longitudinal depression moderately densely and finely punctate (interspaces rugulose); adjacent convex area densely and moderately coarsely punctate, punctures coalescent with striate interspaces. Supraclypeal area sparsely and moderately finely punctate on disc; interspaces imbricate. Malar area longitudinally sparsely and finely punctate; interspaces finely striate. Paraocular area densely and moderately finely punctate (except puncture fine towards antennal socket and near eye); interspaces smooth. Frontal area densely and moderately coarsely punctate; interspaces imbricate. Vertexal area punctures crowded and moderately fine near lateral ocellus; punctures sparser and finer towards eye; interspaces smooth throughout. Mesoscutum and scutellum densely and coarsely punctate; interspaces smooth. Metanotum punctures crowded and moderately fine. Mesepisternum densely and coarsely punctate (except punctures crowded anterior to episternal groove and moderately sparse ventrally); interspaces smooth. Metepisternum with oblique carinae mid-anteriorly; rugose above; imbricate below. Lateral surface of propodeum sparsely and finely punctate; interspaces smooth. Vertical surface of metapostnotum rugulose above. Metasomal terga with smooth



interspaces; T1 finely and sparsely punctate; T2–T5 minutely punctate. Metasomal sterna with imbricate interspaces; S1 sparsely and finely punctate; S2–S3 moderately densely and finely punctate (except punctures sparse mid-longitudinally); S4–S5 densely and finely punctate; S6 densely and moderately finely punctate (except punctures sparse mid-longitudinally).

MALE: Unknown.

**Type material:** *Holotype* ♀ – “RPSP; 12.4157”. “Brasil, RS, Rd. BR 153; 39 km NE Bagé, 30°52'15"S; 53°36'59"W em Fabaceae; 01.xi.2012 E.Almeida & A.Aguiar”. “VOUCHER # 08; Pampas-RS 2012”. “CCDB-24581 A11”. “HOLOTYPE; *Colletes sexangulus* ♀; Ferrari, new species”. {RPSP}.

*Paratype:* **BRAZIL – Rio Grande do Sul:** Santana da Boa Vista, Guaritas, 13/xi/1992, [C. Schlindwein], 1♀, {UFMG}.

**Range:** BRAZIL (Rio Grande do Sul). See also Fig. 33.

**Biogeographical distribution:** Chacoan dominion (Pampean province) at altitudes of 0–400m a.s.l.

**DNA barcode:** Unavailable.

**Floral hosts:** Unknown.

**Etymology:** Allusion to its characteristic hexagonal clypeus.

**Comments:** Apparently a rare species that might be endemic to the Pampas ecoregion in the South American southeast.

# **Key to the *Colletes* species found in Brazil, Paraguay and Uruguay:**

Note: The males of *C. ferenudus* **n. sp.**, *C. imbricatus* **n. sp.** and *C. sexangulus* **n. sp.**, and the female of *C. chicoi* **n. sp.**, are unknown.

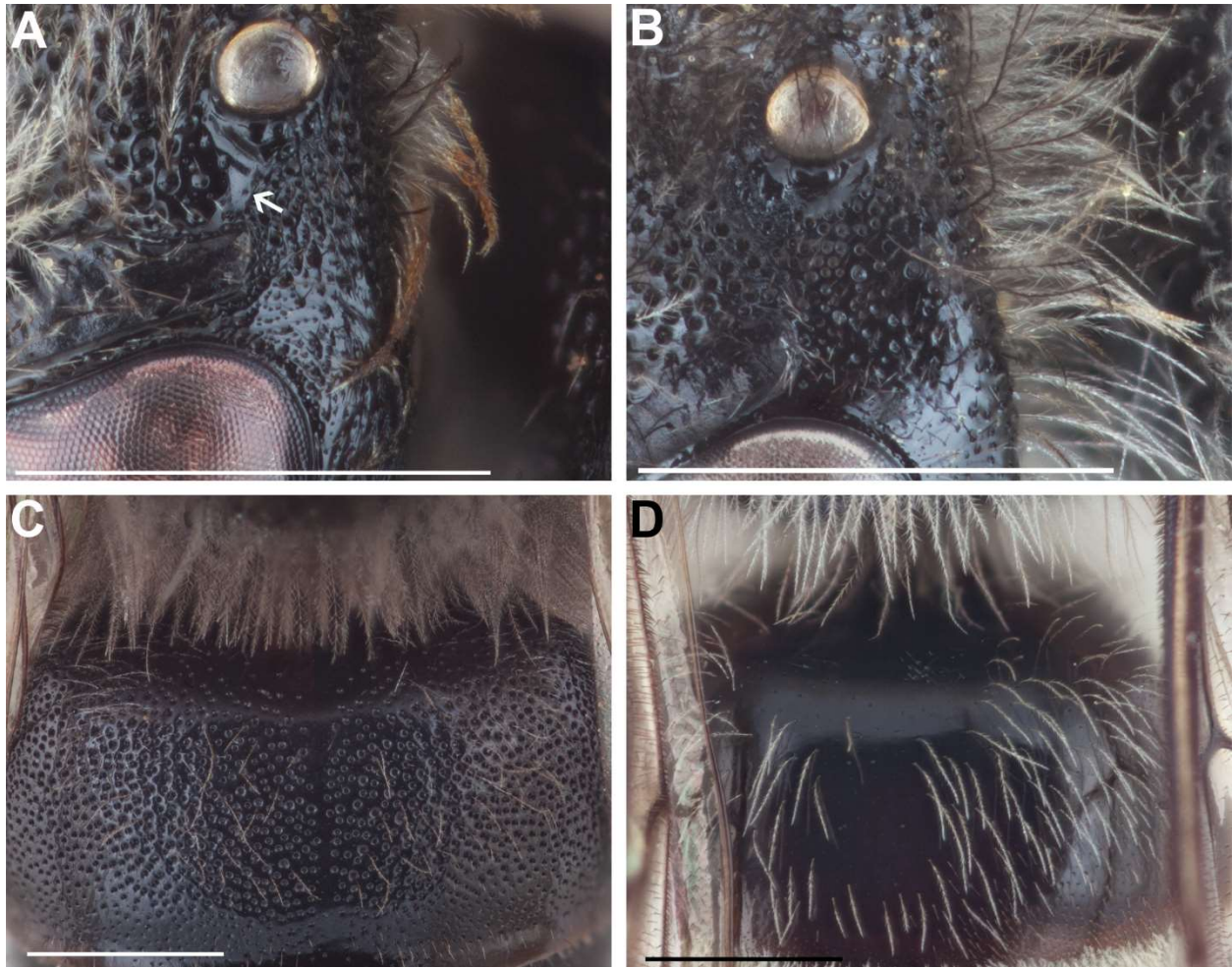
1 Female .....	2
- Male .....	19
2 Mesoscutum with black and off-white hairs intermixed (Figs. 2A, 5A, 10A, 29A, 36A, 40A) ....	3
- Mesoscutum with pale-yellow to bright-orange hairs (Figs. 13A, 15A, 17A, 20A, 23A, 25A, 27A, 34A, 38A, 42A, 44A) .....	8
3 T1–T5 discs metallic-blue (Figs. 10E, 29E) .....	4
- T1–T5 discs black (Figs. 2E, 5E, 36E, 40E) .....	5
4 Clypeus longitudinally and finely striate (Fig. 45A); metanotum with hairs predominantly off-white (Fig. 45C) .....	<i>C. cyaneus</i> Holmberg, 1903
- Clypeus not striate (Fig. 45B); metanotum with hairs predominantly black (Fig. 45D) .....	<i>C. michenerianus</i> Moure, 1956
5 Frontal area with protrusion below lateral ocellus (Fig. 46A); T1 coarsely punctate (Fig. 46C) ..	6
- Frontal area without protrusion below lateral ocellus (Fig. 46B); T1 minutely to finely punctate (Fig. 46D) .....	7
6 Hypostomal carina short and flat (Fig. 47A); paraocular area with hairs predominantly off-white (Fig. 47B) .....	<i>C. argentinus</i> Friese, 1908
- Hypostomal carina produced as a tall, concave lamella in profile (Fig. 47C); paraocular area with hairs predominantly pale-yellow (Fig. 47D) .....	<i>C. rugicollis</i> Friese, 1900



**Figure 45.** Frontal view of head (A–B) and dorsal view of mesosoma (C–D). (A) Clypeus longitudinally and finely striate in *Colletes cyaneus*; (B) clypeus not striate in *C. michenerianus*. (C) Metanotum predominantly with off-white hairs in *C. cyaneus*; (D) metanotum predominantly with black hairs in *C. michenerianus*. Scale bars = 1mm.

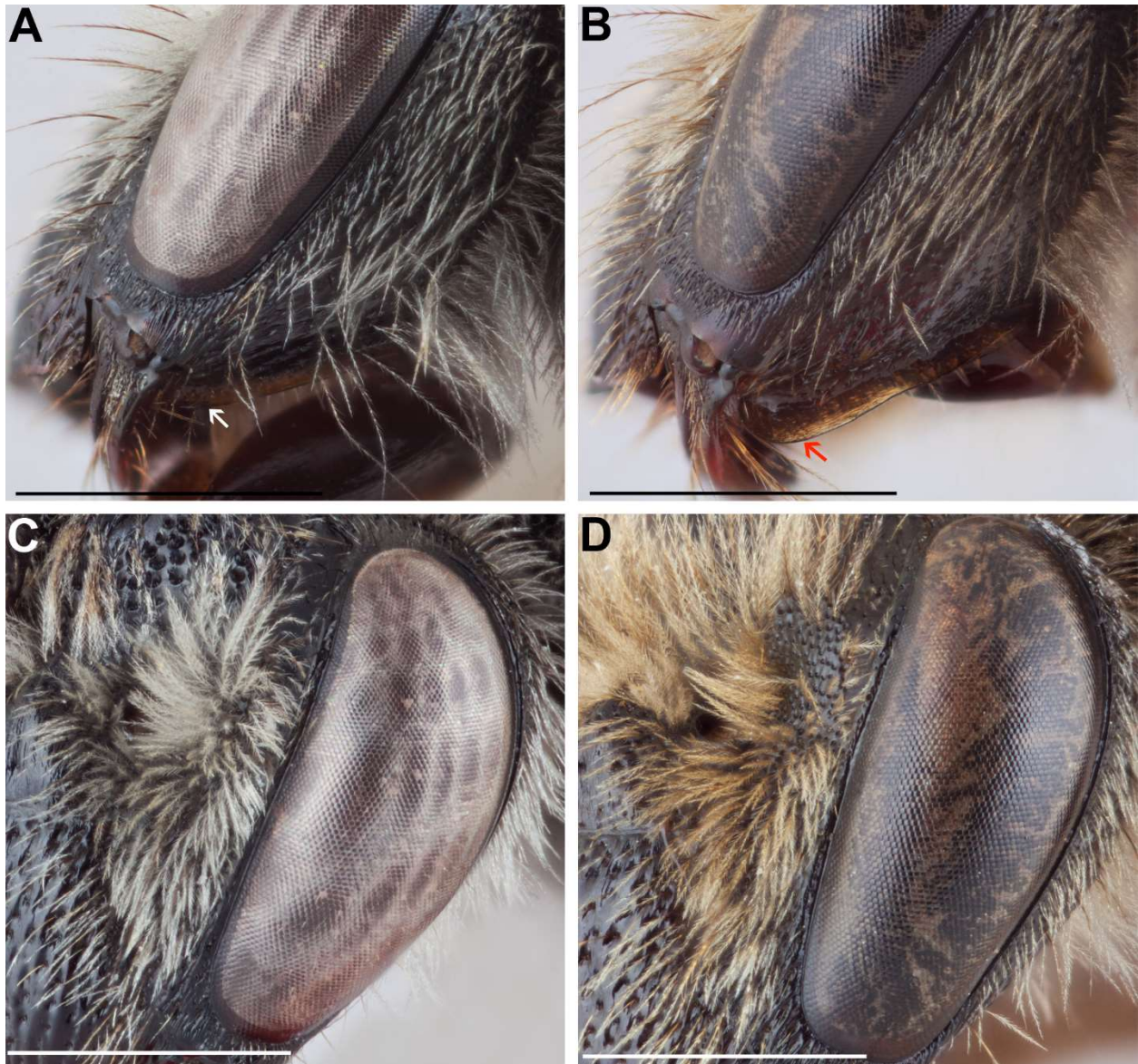
7 Malar area relatively long, 0.8x as long as basal depth of mandible; posterior hind tibial spur ciliate (Fig. 48A) ..... *C. altimontanus* Ferrari & Silveira, 2015  
 - Malar area relatively short, 0.4x as long as basal depth of mandible; posterior hind tibial spur pectinate (Fig. 48B) ..... *C. petropolitanus* Dalla Torre, 1896





**Figure 46.** Latero-dorsal view of head (A–B) and dorsal view of metasoma (C–D). (A) Frontal area with protrusion below lateral ocellus in *Colletes argentinus*; (B) Frontal area without protrusion in *C. petropolitanus*. (C) T1 coarsely punctate in *C. argentinus*; (D) T1 minutely punctate in *C. petropolitanus*. Scale bars = 1mm.

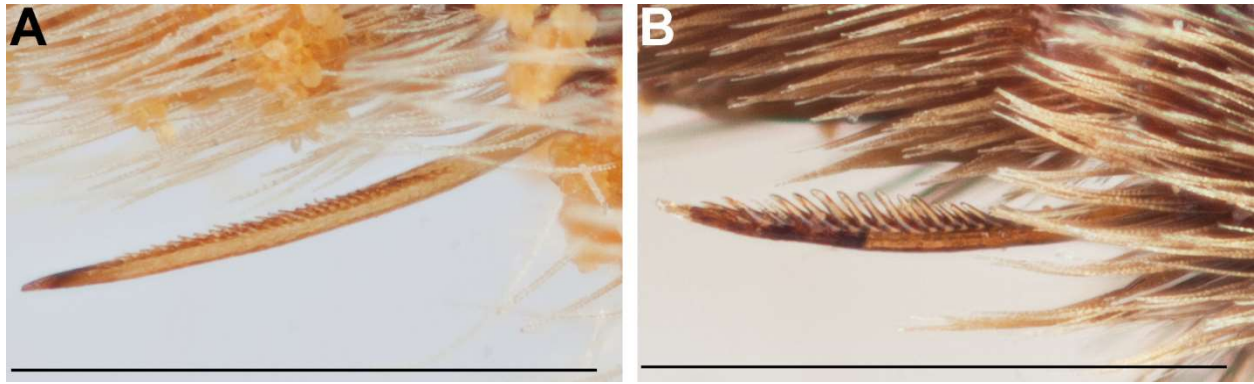
- 8 Mesepisternum with imbricate interspaces (Fig. 49A) ..... 9
- Mesepisternum with smooth interspaces (Fig. 49B) ..... 10
  
- 9 F1 relatively long, 1.5x as long as its apical width; legs black with fuscous hairs (Fig. 13C) ..... *C. ferenudus* **n. sp.**
- F1 relatively short, 1.2x as long as its apical width; legs pale-brown with pale-yellow hairs (Fig. 23C) ..... *C. imbricatus* **n. sp.**



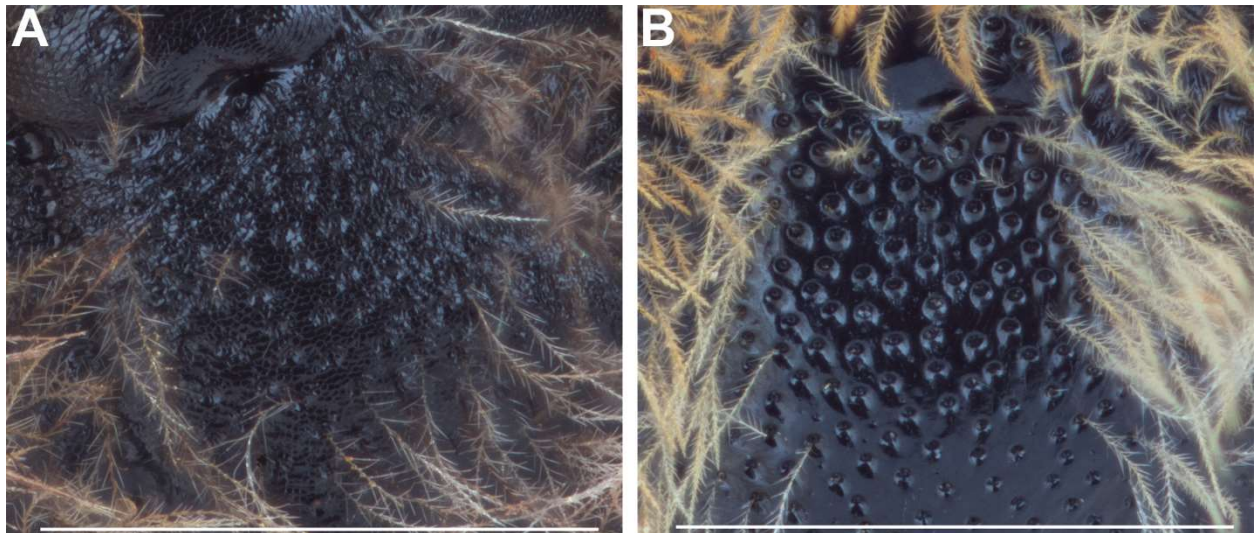
**Figure 47.** Lateral (A–B) and oblique (C–D) views of head. (A) Hypostomal carina (white arrow) short and flat in *Colletes argentinus*; (B) hypostomal carina (red arrow) produced as a tall concave lamella in *C. rugicollis*. (C) Paraocular area predominantly with off-white hairs in *C. argentinus*; (D) paraocular area predominantly with pale-yellow hairs in *C. rugicollis*. Scale bars = 1mm.

10 T2–T5 discs without appressed plumose hairs (Fig. 50A) .....	11
- T2–T5 discs covered with appressed plumose hairs (Fig. 50B) .....	12





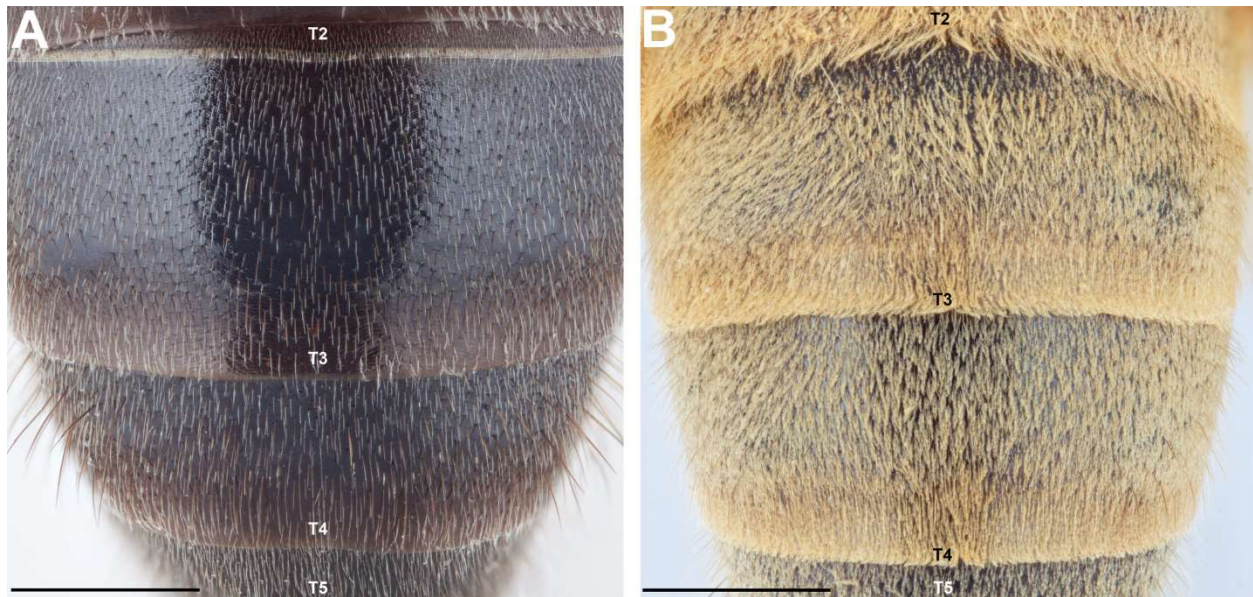
**Figure 48.** Inner view of the posterior spur of hind tibia. (A) Spur ciliate in *Colletes altimontanus*; (B) spur pectinate in *C. petropolitanus*. Scale bars = 1mm.



**Figure 49.** Lateral view of mesosoma. (A) Mesepisternum with imbricate interspaces in *Colletes ferenudus* n. sp.; (B) mesepisternum with smooth interspaces in *C. rufipes*. Scale bars = 1mm.

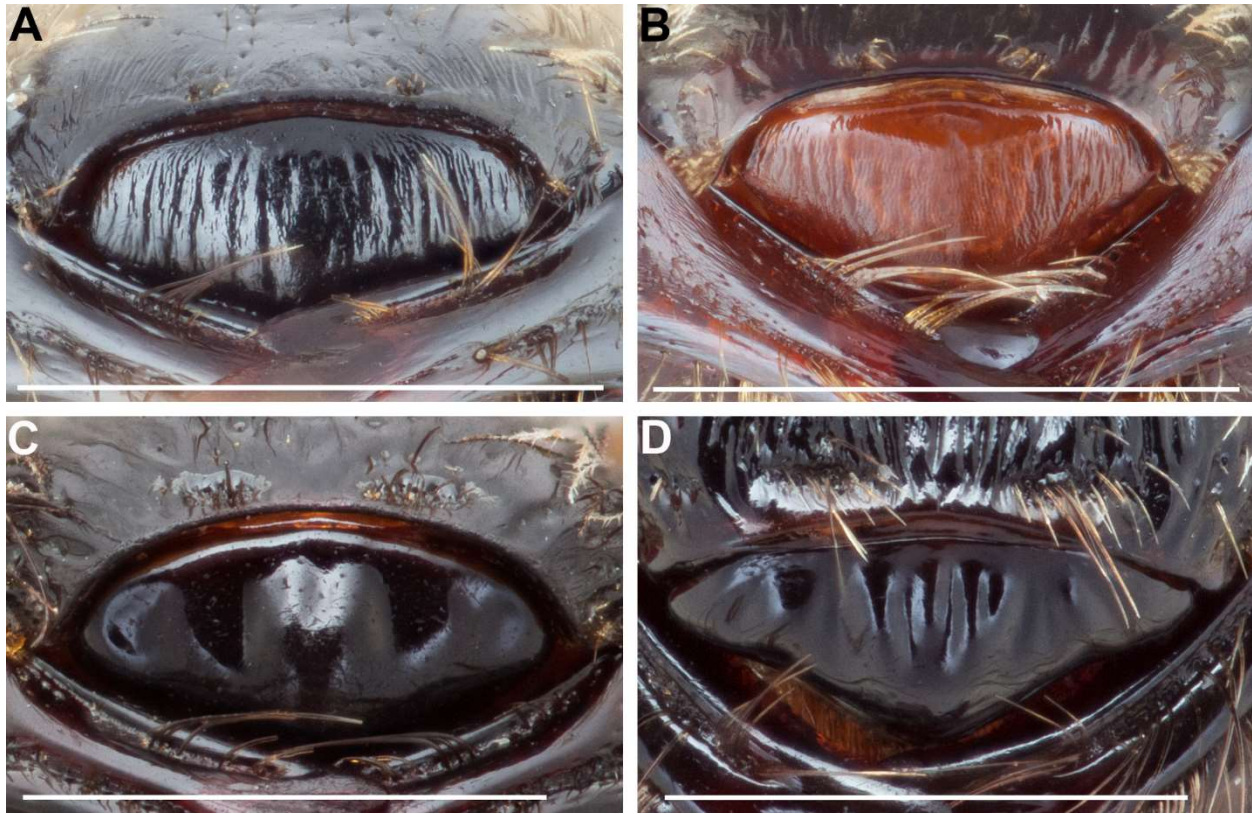
- 11 Relatively small bees, head width 3.0mm; malar area distinctly shorter, 0.2x as long as basal depth of mandible ..... *C. hawkingi* n. sp.  
 - Relatively large bees, head width 3.7mm; malar area distinctly longer, 0.9x as long as basal depth of mandible ..... *C. kerri* Moure, 1956





**Figure 50.** Dorsal view of metasoma. (A) T2–T5 discs without appressed plumose hairs in *Colletes ferenudus* **n. sp.**; (B) T2–T5 discs covered with appressed plumose hairs in *C. rufipes*. Scale bars = 1mm.

- 12 Labrum flat medially (Figs. 51A, 51B) ..... 13  
 - Labrum either convex (Fig. 51C) or concave (Fig. 51D) medially ..... 14
- 13 Labrum black (Fig. 51A); F1 relatively long, 1.9x as long as its apical width; legs black (Fig. 15A) ..... *C. flagellaris* **n. sp.**  
 - Labrum reddish-brown (Fig. 51B); F1 relatively short, 1.4x as long as its apical width; legs dark-orange (Fig. 38A) ..... *C. rufipes* Smith, 1879
- 14 Hypostomal carina produced as a tall, concave lamella in profile (Fig. 47B); mesoscutum anterolaterally and pronotal lobe with distinctive patch of bright-orange hairs that strongly contrasts with pale-yellow pubescence elsewhere on dorsum of mesosoma (Figs. 31A) ..... *C. ornatus* Schrottky, 1902  
 - Hypostomal carina short and flat (Fig. 47A); mesoscutum anterolaterally and pronotal lobe with hairs of the same colour as those elsewhere on dorsum of mesosoma (Figs. 17E, 27E, 34E, 42E) ..... 15



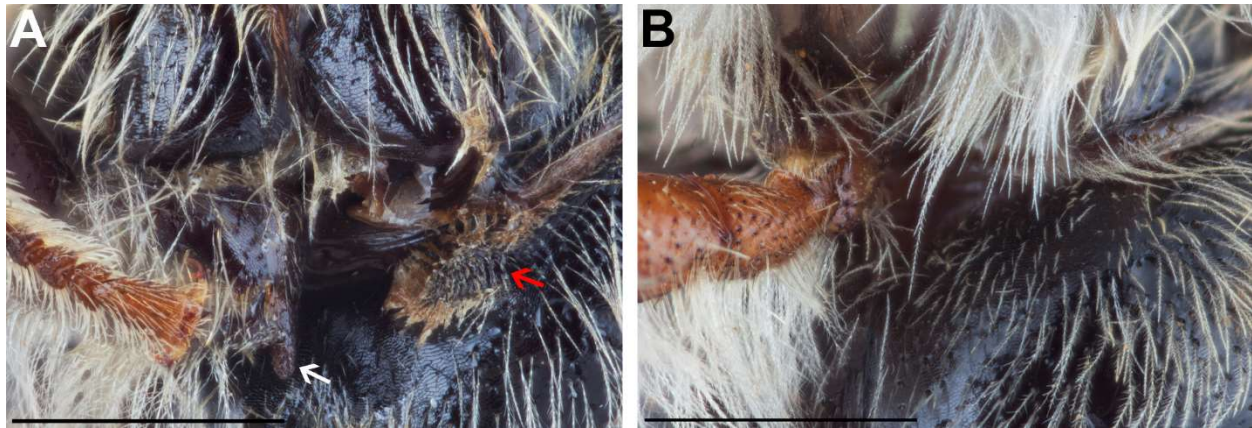
**Figure 51.** Ventral view of head. Labral mid area flat in (A) *Colletes flagellaris* **n. sp.** and (B) *C. rufipes*, convex in (C) *C. michenerianus*, and concave in (D) *C. cyaneus*. Scale bars = 1mm.

15 Malar area relatively long, at least 1.2x as long as basal depth of mandible ..... 16  
 - Malar area relatively short, at most 0.8x as long as basal depth of mandible ..... 18

16 Relatively small bees, head width approximately 2.5mm; metasomal terga with pale-brown discs (Fig. 42A, 42E) ..... *C. sertanicola* **n. sp.**  
 - Relatively large bees, head width between 3.0–3.5mm; metasomal terga with black discs (Fig. 17A, 17E, 34A, 34E) ..... 17

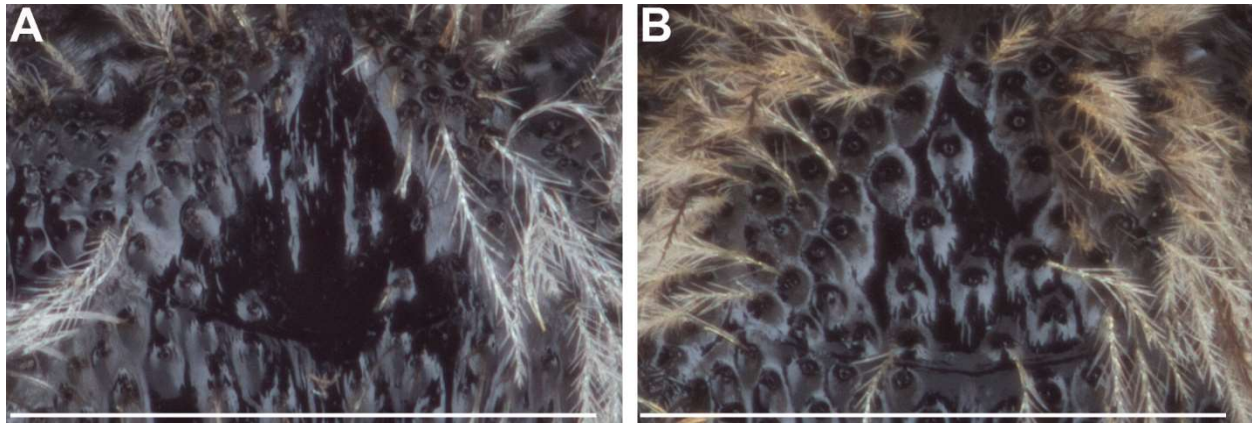
17 Legs black (Fig. 17A); marginal zones of T1–T5 dark-brown (Fig. 17E) .....  
 ..... *C. furfuraceus* Holmberg, 1886  
 - Legs pale-brown (Fig. 34A); marginal zones of T1–T5 pale-brown (Fig. 34E) .....  
 ..... *C. pampeanus* **n. sp.**





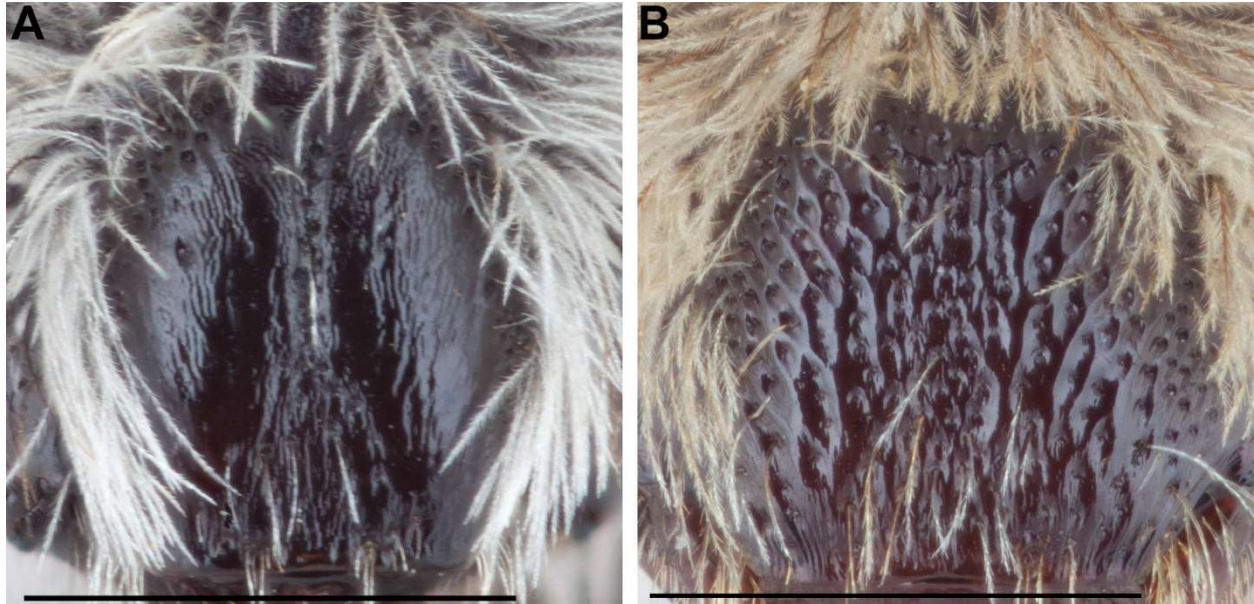
**Figure 52.** Ventral view of mesosoma. (A) Front coxa with spine (white arrow), and mesepisternum ventrally with protrusion (red arrow), in *Colletes meridionalis*; (B) front coxa without spine, and mesepisternum without protrusion, in *C. rufipes*. Scale bars = 1mm.

- 18 Mesepisternum ventrally, near ventral end of episternal groove, with protrusion surrounded by appressed short hairs (Fig. 52A); front coxa with strong spine (Fig. 52A) ..... *C. meridionalis* Schrottky, 1902
- Mesepisternum ventrally, near ventral end of episternal groove, without protrusion (Fig. 52B); front coxa without spine (Fig. 52B) ..... *C. sexangulus* n. sp.
- 19 Mesoscutum with black and off-white hairs intermixed (Figs. 2B, 5B, 10B, 29B, 36B, 40B) ..... 20
- Mesoscutum with pale-yellow to bright-orange hairs (Figs. 8C, 15B, 17B, 20B, 25B, 27B, 34B, 38B, 42B) ..... 25
- 20 T1–T5 discs metallic-blue (Figs. 10F, 29F) ..... 21
- T1–T5 discs dark-brown to black (Figs. 8A, 17F, 20F, 25F, 27F, 34F, 38F, 42F) ..... 22
- 21 Malar area relatively long, 1.8x as long as basal depth of mandible; legs with off-white hairs (Figs. 10B) ..... *C. cyaneus* Holmberg, 1903
- Malar area relatively short, 1.5x as long as basal depth of mandible; legs with fuscous to black hairs (Figs. 29B) ..... *C. michenerianus* Moure, 1956



**Figure 53.** Frontal view of head. (A) Supraclypeal area sparsely punctate in *Colletes argentinus*; (B) supraclypeal area densely punctate in *C. rugicollis*. Scale bars = 1mm.

- 22 Frontal area with protrusion below lateral ocellus (Fig. 46A); T1 coarsely punctate (Fig. 46C) ..... 23
- Frontal area without protrusion below lateral ocellus (Fig. 46B); T1 minutely to moderately finely punctate (Fig. 46D) ..... 24
- 23 Hypostomal carina short and flat (Fig. 47A); supraclypeal area sparsely punctate (Fig. 53A) ..... *C. argentinus* Friese, 1908
- Hypostomal carina produced as a tall, concave lamella in profile (Fig. 47B); supraclypeal area densely punctate (Fig. 53B) ..... *C. rugicollis* Friese, 1900
- 24 Clypeus largely impunctate (Fig. 54A); malar area relatively long, 1.4x as long as basal depth of mandible ..... *C. altimontanus* Ferrari & Silveira, 2015
- Clypeus densely punctate (Fig. 54B); malar area relatively short, 0.8x as long as basal depth of mandible ..... *C. petropolitanus* Dalla Torre, 1896
- 25 T2–T5 discs covered with appressed plumose hairs (Fig. 50B) ..... 26
- T2–T5 discs without appressed plumose hairs (Fig. 50A) ..... 27



**Figure 54.** Frontal view of head. (A) Clypeus largely impunctate in *Colletes altimontanus*; (B) clypeus densely punctate in *C. petropolitanus*. Scale bars = 1mm.

- 26 Labrum black (Fig. 51A); legs black (Fig. 15B) ..... *C. flagellaris* **n. sp.**  
 - Labrum reddish-brown (Fig. 51B); legs dark-orange (Fig. 38B) ..... *C. rufipes* Smith, 1879
- 27 T1 pale-brown (Fig. 55A) or dark-brown (Fig. 55B) anteriorly ..... 28  
 - T1 black anteriorly (Fig. 55C) ..... 29
- 30 Hypostomal carina produced as a tall, concave lamella in profile (Fig. 47B); mesoscutum anterolaterally and pronotal lobe with distinctive patch of pale-yellow hairs that strongly contrasts with off-white pubescence elsewhere on dorsum of mesosoma (Fig. 31A) .....  
 ..... *C. ornatus* Schrottky, 1902  
 - Hypostomal carina short and flat (Fig. 47A); mesoscutum anterolaterally and pronotal lobe with hairs of the same colour as those elsewhere on dorsum of mesosoma (Figs. 25F, 34F) ..... 31





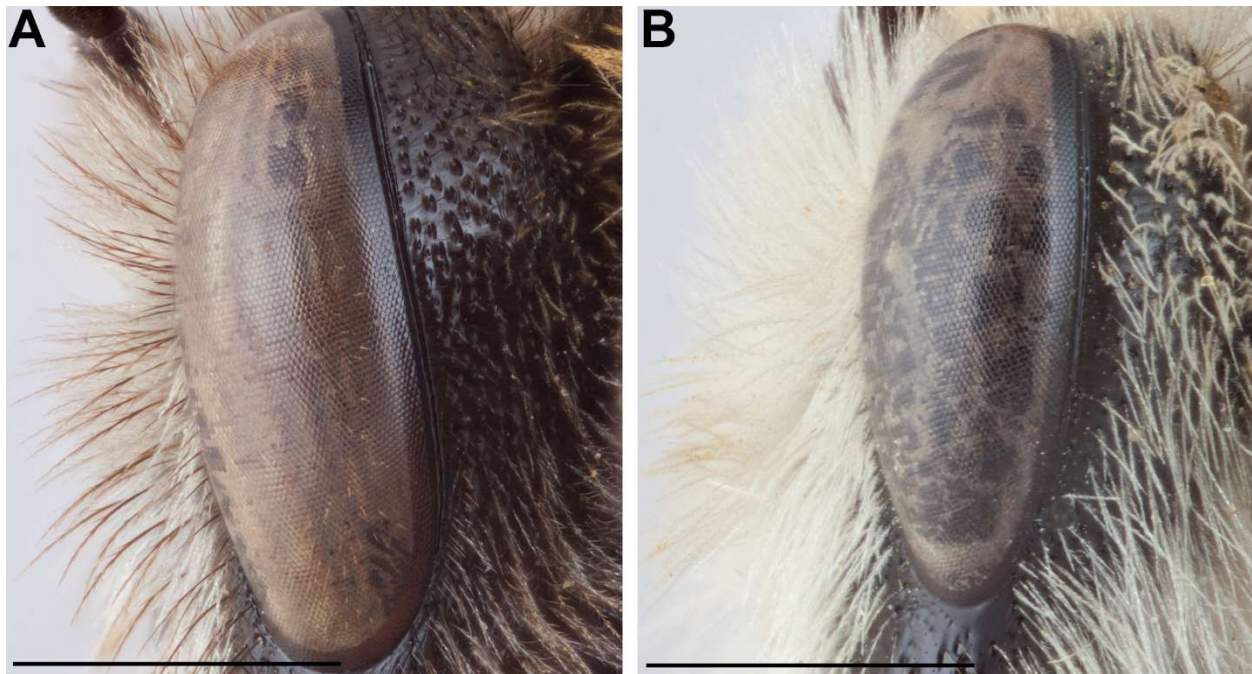
**Figure 55.** Dorsal view of metasoma. (A) T1 pale-brown anteriorly in *Colletes chicoi* **n. sp.**; (B) T1 dark-brown anteriorly in *C. sertanicola* **n. sp.**; (C) T1 black anteriorly in *C. meridionalis*. Scale bars = 1mm.

31 Malar area distinctly shorter, 0.8x as long as basal depth of mandible; labrum flat medially (Fig. 51A) ..... *C. kerri* Moure, 1956  
 - Malar area distinctly longer, 2.0x as long as basal depth of mandible; labrum concave medially (Fig. 51D) ..... *C. pampeanus* **n. sp.**

32 Malar area distinctly shorter, 0.2x as long as basal depth of mandible; T1 sparsely punctate (Fig. 57A) ..... *C. hawkingi* **n. sp.**  
 - Malar area distinctly longer, at least as long as basal depth of mandible; T1 moderately densely punctate (Fig. 57B) ..... 33

33 Mesepisternum ventrally, near ventral end of episternal groove, without protrusion surrounded by appressed short hairs (Fig. 52B); tarsi dark-brown to black (Fig. 17B) ..... *C. furfuraceus* Holmberg, 1886  
 - Mesepisternum ventrally, near ventral end of episternal groove, with protrusion surrounded by appressed short hairs (Fig. 52A); tarsi pale-brown (Fig. 27B) .... *C. meridionalis* Schrottky, 1902





**Figure 56.** Lateral view of head. (A) Paraocular area with intermixed black and off-white hairs in *Colletes kerri*; (B) paraocular area with only pale-yellow hairs in *C. meridionalis*. Scale bars = 1mm.

## Discussion

This is the most comprehensive revisionary study of *Colletes* in Brazil, Paraguay, and Uruguay to date, and as a result the number of species known to occur in these three countries has increased from 11 to 19. All 19 species are found in Brazil (13 of them are endemic), two (*C. petropolitanus* and *C. ornatus*) are found in both Brazil and Paraguay, and *C. argentinus* is found in all three countries. However, some of the species recorded from southern Brazil—*C. cyaneus*, *C. ferenudus* **n. sp.**, *C. furfuraceus*, *C. imbricatus* **n. sp.**, *C. meridionalis* and *C. pampeanus* **n. sp.**—are expected to occur in Paraguay and/or Uruguay given the proximity of some collection localities to the borders of the two countries.

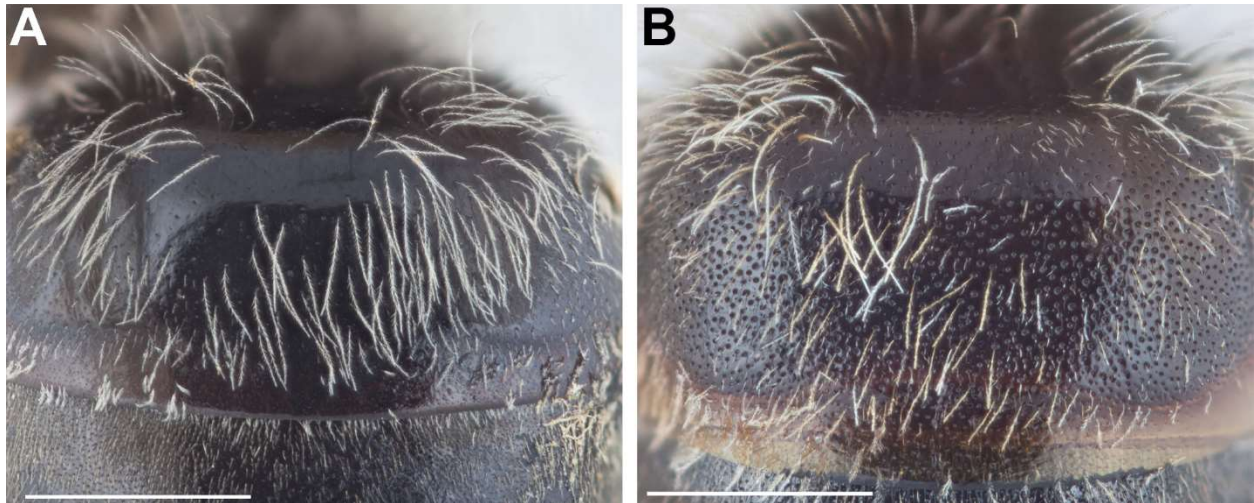
The eight new species described herein can be reliably identified with the aid of the key and diagnoses provided herein, two of which in particular (*C. chicoi* **n. sp.** and *C. sertanicola* **n. sp.**) stand out as, unusually for *Colletes*, they exhibit brownish as opposed to black colouration on the metasoma (Fig. 55). DNA barcoding was useful not only in helping diagnosing some of

the new species, but also providing further support for recognizing *C. argentinus* as a separate species from *C. rugicollis*. Regrettably, the identity of *C. punctatissimus* (the male holotype of which is lost) remains unclear, and therefore I was unable to verify whether this species is either a junior synonym of *C. rugicollis* (as suggested by Moure & Urban 2002) or a senior synonym of *C. argentinus* (as speculated by Ferrari & Silveira 2015).

Whereas subgenera and species groups have been proposed for the North American and Old World *Colletes* (e.g. Stephen 1954; Warncke 1978), no intrageneric subdivision is available for the South American fauna of the genus. While it is tempting to organize highly diverse genera such as *Colletes*, even if informally, into species groups based on easily observable similarities, non-monophyletic species groups can obfuscate our understanding of the actual phylogenetic relationships among the species. Therefore, an intrageneric classification for the South American *Colletes* should not be provided until a comprehensive phylogeny for these interesting bees is available (see Chapter 5).

## Acknowledgements

I would like to thank the curators and collection managers listed in “Material and Methods” for the loans of the studied bees. In particular, I thank Gabriel Melo, David Notton and Claire Villemant for allowing me to study the type specimens of *Colletes* deposited in the repositories under their care. I am also very grateful to Arturo Roig-Alsina for sending me pictures of the future neotypes of *C. cyaneus* and *C. furfuraceus*, Claus Rasmussen and Carlos Garófalo for donating specimens of *C. rugicollis* and *C. rufipes*, respectively. I am deeply indebted to Laurence Packer for the wise supervision provided. Thomas Onuferko kindly tested the taxonomic key, and Daniela Hernandez gently proofed the Spanish version of the abstract. Michael Kuhlmann and Jason Gibbs provided thoughtful comments and suggestions on an earlier version of this manuscript. The pictures of this study were taken with the imaging system purchased through a Canadian Foundation for Innovation award through Canadensys. This research was conducted thanks to funds provided by CAPES (BEX 11875/13-5) and the Faculty of Graduate Studies of York University.



**Figure 57.** Dorsal view of metasoma. (A) T1 sparsely punctate in *Colletes hawkingi* n. sp.; (B) T1 moderately densely punctate in *C. meridionalis*. Scale bars = 1mm

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## Appendix I: Supplementary tables

**Table S1.** Collection data, sex, and BOLD-related information of the barcoded specimens of each *Colletes* species.

Species	Locality	Sex	BOLD sample ID	BOLD BIN
<i>Colletes argentinus</i>	Argentina, Catamarca, 20km N of Andalgalá	♀	CCDB-15259-C03	BOLD: AAI9260
	Argentina, Corrientes, Parque Nacional Mburucuya	♂	ARG-6829-32	BOLD: AAI9260
	Brazil, Paraná, São Matheus do Sul	♀	CCDB-22009-G07	BOLD: AAI9260
	Brazil, Rio Grande do Sul, 29km S of Santana Livramento	♀	CCDB-24582-H01	BOLD: AAI9260
	Paraguay, Guairá, Reserva Ybytyruzó	♂	B1401-F03	BOLD: AAI9260
	Paraguay, Paraguairí, Paraguairí	♂	B1401-F02	BOLD: AAI9260
	Paraguay, Paraguairí, Paraguairí	♂	B1401-F02	BOLD: AAI9260
<i>Colletes cyaneus</i>	Brazil, Rio Grande do Sul, 12km NNE of Pedras Altas	♂	CCDB-30344-E01	BOLD: ADI1118
	Brazil, Rio Grande do Sul, Santana do Livramento	♀	CCDB-30344-D09	BOLD: ADI1118
<i>Colletes ferenudus</i> n. sp.	Brazil, Rio Grande do Sul, 12km NNE of Pedras Altas	♀	CCDB-24581-A09	BOLD: ACV1831
	Brazil, Rio Grande do Sul, Minas de Camaquã	♀	CCDB-22009-F06	BOLD: ACV1831
	Brazil, Rio Grande do Sul, Santana do Livramento	♀	CCDB-24581-D01	BOLD: ACV1831
	Brazil, Rio Grande do Sul, Santana do Livramento	♀	CCDB-30344-E05	BOLD: ACV1831
	Brazil, Rio Grande do Sul, Santana do Livramento	♀	CCDB-30344-E05	BOLD: ACV1831
<i>Colletes flagellaris</i> n. sp.	Brazil, Rio de Janeiro, Itatiaia	♂	CCDB-30383-D07	Non-BIN-compliant
<i>Colletes hawkingi</i> n. sp.	Brazil, Ceará, Santana do Cariri	♀	CCDB-30383-D05	Non-BIN-compliant
<i>Colletes meridionalis</i>	Brazil, Minas Gerais, Serra do Salitre	♀	CCDB-24581-C10	BOLD: ADF9673
	Brazil, Minas Gerais, Serra do Salitre	♂	CCDB-24582-H07	BOLD: ADF9673
	Brazil, Minas Gerais, Serra do Salitre	♂	CCDB-30345-D11	BOLD: ADF9673
	Brazil, Rio Grande do Sul, Santana do Livramento	♀	CCDB-30383-B05	BOLD: ADF9673
	Brazil, Rio Grande do Sul, Santana do Livramento	♀	CCDB-30383-B05	BOLD: ADF9673
<i>Colletes petropolitanus</i>	Brazil, Minas Gerais, Poços de Caldas	♀	CCDB-24581-C04	BOLD: AAR9968
	Brazil, Minas Gerais, Poços de Caldas	♂	CCDB-30345-D09	BOLD: AAR9968
	Brazil, Santa Catarina, Campo Alegre	♀	CCDB-24582-H11	BOLD: AAR9968
	Paraguay, San Pedro, Cororo	♀	B1401-F04	BOLD: AAR9968
	Paraguay, San Pedro, Cororo	♀	B1401-F04	BOLD: AAR9968
<i>Colletes rufipes</i>	Brazil, Minas Gerais, São Gonçalo do Rio das Pedras	♂	CCDB-24852-H03	BOLD: ADG1971
<i>Colletes rugicollis</i>	Brazil, Paraná, Piraquara	♂	CCDB-30383-C04	BOLD: ACV1581
	Brazil, Paraná, São Mateus do Sul	♀	CCDB-22009-G06	BOLD: ACV1581
	Brazil, Santa Catarina, Pomerode	♂	CCDB-30383-C02	BOLD: ACV1581

**Table S2.** List of the *Colletes* species and their floral hosts reported in this study for the first time.

<b>Species</b>	<b>Plant species</b>	<b>Plant family</b>	<b>Locality</b>	<b>Month</b>
<i>Colletes altimontanus</i>	<i>Eriope crassipes</i>	Lamiaceae	Brazil, Pernambuco, Parque Nacional do Catimbau	September
	<i>Hypenia salzmännii</i>	Lamiaceae	Brazil, Pernambuco, Parque Nacional do Catimbau	June
<i>Colletes ferenudus</i> <b>n. sp.</b>	<i>Blumenbachia insignis</i>	Loasaceae	Brazil, Rio Grande do Sul, Caçapava do Sul	October
<i>Colletes furfuraceus</i>	<i>Adesmia trijuga</i>	Leguminosae	Argentina, Catamarca, Cuesta Minas Capillitas	December
	<i>Atamisquea emarginata</i>	Capparaceae	Argentina, Catamarca, Andalgalá	November
	<i>Prosopis nigra</i>	Leguminosae	Argentina, Catamarca, locality not specified	November
<i>Colletes imbricatus</i> <b>n. sp.</b>	<i>Blumenbachia insignis</i>	Loasaceae	Brazil, Rio Grande do Sul, Caçapava do Sul	October
<i>Colletes meridionalis</i>	<i>Cuphea</i> sp.	Lythraceae	Brazil, Minas Gerais, Serra do Cipó	February
<i>Colletes michenerianus</i>	<i>Prosopis</i> sp.	Leguminosae	Brazil, Paraná, Guarapuava	September
<i>Colletes petropolitanus</i>	<i>Baccharis dracunculifolia</i>	Compositae	Brazil, Santa Catarina, Pomerode	April
<i>Colletes rugicollis</i>	<i>Hyptis</i> sp.	Lamiaceae	Brazil, Santa Catarina, Pomerode	November
	<i>Mikania cordifolia</i>	Compositae	Brazil, Santa Catarina, Pomerode	March
	<i>Solidago chilensis</i>	Compositae	Brazil, Santa Catarina, São Martinho	March



## Chapter 5: The evolutionary history of *Colletes* Latreille (Hymenoptera: Colletidae): molecular phylogeny, biogeography and implications for a global intrageneric classification

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### Abstract

*Colletes* Latreille (Hymenoptera: Colletidae) is a megadiverse genus with *c.* 520 valid species of polyester bees distributed in all biogeographic realms, except Australasia and Antarctica. In this study, a comprehensive dated phylogeny for *Colletes* is provided, based on Bayesian analysis of DNA sequence data of six loci: 28S rDNA, cytochrome c oxidase subunit 1, elongation factor-1 $\alpha$  copy F2, long-wavelength rhodopsin, RNA polymerase II and *wingless*. In total, our multilocus matrix consists of 4824 aligned base pairs for 143 species, including 112 *Colletes* species plus 31 outgroups (one stenotritid and a diverse array of colletids representing all subfamilies). Overall, analyses of each of the six single-locus datasets resulted in poorly resolved consensus trees with conflicting phylogenetic signal. Our multilocus analyses provide strong support for the monophyly of *Colletes* and show that it consists of five major clades. The implications of our phylogenetic results for future intrageneric classification attempts regarding the *Colletes* of the world are discussed. Herein, we propose species groups for the Neotropical species of *Colletes*, the only major biogeographic realm for which no species groups have been proposed to date. Our dating analysis indicate that *Colletes* diverged from its sister taxon, *Hemicotelles* Toro and Cabezas, in the early Oligocene and that the extant lineages of the former began diversifying only in the late Oligocene. According to our biogeographic reconstruction, *Colletes* originated in the Neotropics (most likely within South America) and then geodispersed to the Nearctic very early in its evolutionary history. A very early geodispersal to the Old World

occurred soon after colonization of the Northern Hemisphere. Lastly, the historical biogeography of *Colletes* is analyzed in the light of available geological and palaeoenvironmental data.

## Introduction

With *c.* 520 valid described species, the polyester bee genus *Colletes* Latreille (Hymenoptera: Colletidae) is the seventh most diverse among all bee genera and the second among colletids after *Hylaeus* Fabricius (Ascher and Pickering, 2019). The actual species richness of *Colletes*, however, has been estimated to be closer to 700 (Kuhlmann et al., 2009). In fact, the genus has received a significant amount of taxonomic attention over the past decade resulting in a large number of new species (>70 spp.) being described (Kuhlmann, 2014a, b; Kuhlmann and Proshchalykin, 2011, 2013, 2014a, 2015, 2016; Kuhlmann and Pauly, 2013; Proshchalykin and Kuhlmann, 2015; Niu et al., 2013a, b, 2014; Ferrari and Silveira, 2015; Hall et al., 2016; Balboa et al., 2017; Ferrari, 2017, 2019). Unlike most colletid genera, most of which have a comparatively restricted geographic distribution, *Colletes* is found in all biogeographic realms except Australasia and Antarctica (Michener, 1989, 2007; Kuhlmann et al., 2009; Bystriakova et al., 2018; Ascher and Pickering, 2019). A recent analysis of the environmental factors determining the global distribution of the Colletinae demonstrated that the peaks in their species richness are found in the semi-arid regions located at middle latitudes (Bystriakova et al., 2018). Contrary to *Colletes*, the other genera of Colletinae—*Hemicotelles* Toro and Cabezas (2 spp.), *Mourecotelles* Toro and Cabezas (12 spp.) and *Xanthocotelles* Toro and Cabezas (11 spp.)—are all confined to the Neotropics, most of them to the subtropical and temperate portions of Chile and Argentina (Moure et al., 2007, 2012). It is important to emphasize that the generic classification of Colletinae is controversial, with the number of genera accepted as valid varying substantially among authors (Toro and Cabezas, 1977, 1978; Michener, 1989, 2007; Moure and Urban, 2002; Moure et al., 2007, 2012; Ascher and Pickering, 2019; Chapter 3).

*Colletes* are typically robust, mid-sized bees with relatively dense pubescence in comparison with most colletids, other than the Diphaglossinae (Michener, 1989, 2007). Morphological synapomorphies supporting the monophyly of the genus include: the subhorizontal surface of the metapostnotum with a series of longitudinal carinae or sinuous striae in both sexes (unique within Colletinae), forewing with a sigmoidal second recurrent vein in both

sexes (unique among all bees), and T1 subequal in length to T2 in the males (unique within Colletinae) (Chapter 2). *Colletes* is also monophyletic according to maximum parsimony (Kuhlmann et al., 2009) and Bayesian (Almeida and Danforth, 2009; Almeida et al., 2012, 2019) analyses of DNA sequence data; the former publication provided the most comprehensive phylogeny for *Colletes* so far (91 spp.; Kuhlmann et al., 2009).

With the exception of the subgenus *Ptilopoda* Friese which was erected for an unusual species (*C. maculipennis* Friese [= *C. spilopterus* Cockerell]) with spotted wings from Central America (Friese, 1921), no intrageneric classification for the Neotropical *Colletes* is available to date (Michener, 2007; Kuhlmann et al., 2009). All subgroups proposed within the genus over the 20<sup>th</sup> century—the species groups defined by Noskiewicz and Stephen, as well as all other subgenera, namely, *Albocolletes* Warncke, *Denticolletes* Noskiewicz, *Elecolletes* Warncke, *Nanocolletes* Warncke, *Pachycolletes* Bischoff, *Rhinocolletes* Cockerell and *Simcolletes* Warncke—cover exclusively the Palaearctic and/or Nearctic faunas (Noskiewicz, 1936; Stephen, 1954; Stoeckhert, 1954; Warncke, 1978; Kuhlmann et al., 2009). All subgenera were subsequently ignored with the justification that they had been described for either single unusual species (*Denticolletes*, *Ptilopoda* and *Rhinocolletes*), or for artificial groups of rather ordinary species (*Pachycolletes* and Warncke’s subgenera) with restricted geographic distribution in the western Palaearctic (Michener, 1989, 2007). More recently, Kuhlmann et al. (2009) reassessed the available subgenera based on their phylogenetic results; however, a limited sampling with regards to the Neotropics prevented those authors from elucidating the little-known relationships among the lineages found there. In fact, the Neotropical fauna of *Colletes* has historically received much less taxonomic attention in comparison with those from the other biogeographic realms (Michener, 2007: 169). However, a series of recently published revisions have significantly augmented our knowledge on the Neotropical *Colletes* thus reducing the taxonomic impediment pertaining to them (Toro, 1999; Genaro, 2003; Ferrari & Silveira, 2015; Balboa et al., 2017; Ferrari, 2017, 2019).

Resolving the relationships among the Neotropical species of *Colletes*—in particular those found in South America where the genus most likely arose (Michener, 1979, 1989, 2007; Kuhlmann et al., 2009; Almeida et al., 2012; Ferrari and Packer, *in prep.*)—would be pivotal in attempting to understand the historical biogeography of the genus as a whole. The hypothesis that the ancestral *Colletes* may have inhabited South America was first suggested in the late 70’s

(Michener, 1979), but only recently has it become supported by phylogenetic evidence (Kuhlmann et al., 2009; Almeida et al., 2012). It has been hypothesized that from South America *Colletes* spread to North America and then to the Old World (Kuhlmann *et al.*, 2009). The crown age of *Colletes* has been dated to the early Oligocene (*c.* 30 million years ago [Mya]; Almeida et al., 2012) approximately simultaneous with the complete fragmentation of Gondwana (Upchurch, 2008). Molecular biogeographic studies have revealed that the processes which culminated in the formation of the Southern continents (Africa, Antarctica, Oceania and South America) played an important role in the diversification of many animal groups (*e.g.* ratites [Cooper et al., 2001], chironomids [Krosch et al., 2011], osteoglossiform fishes [Lavoué, 2016], frogs [Feng et al., 2017]), including bees (*e.g.* megachilids [Litman et al., 2011]; colletids [Almeida et al., 2012, 2019]). However, if the extant *Colletes* actually began diversifying after South America had been completely isolated, it appears safe to assume that the biotic and abiotic factors taking place within the continent at the time, rather than movements of continents, must have been the main drivers of the initial diversification of the genus.

In this study, the evolutionary and biogeographic histories of *Colletes* are investigated. Here we provide a comprehensive phylogeny for the genus based on Bayesian analyses of nuclear and mitochondrial DNA data for 112 species, representing groupings from throughout the range of the genus. We do this with the following objectives: (i) to elucidate the little known relationships among the New World lineages of *Colletes* to serve as the basis for future systematic studies; (ii) to assess the validity of the currently available subgenera from the Old World; and (iii) to reconstruct a biogeographic scenario that explains the current distribution of the genus around the globe in the light of geological and palaeoenvironmental data.

## **Material and methods**

### ***Taxon sampling and specimens studied***

The subfamilial classification of Colletidae adopted herein is that of Almeida et al. (2019), in which *Paracolletes* Smith is a member of Diphaglossinae, *Callomelitta* Smith is considered in its own subfamily, and the other genera traditionally classified in Paracolletinae (*e.g.* Michener, 2007, as Paracolletini) are considered to belong to Neopasiphaeinae. Our taxon

sampling comprises 143 species, 31 of which are outgroups and 112 are *Colletes* (Table S1). Among the outgroups, 22 species belong in the following subfamilies of Colletidae: Callomelittinae (1 sp.), Diphaglossinae (3 spp.), Euryglossinae (3 spp.), Hylaeinae (4 spp.), Neopasiphaeinae (5 spp.), Scapterinae (2 spp.) and Xeromelissinae (4 spp.). We also sampled eight species of the other genera of Colletinae—*Hemicotelles* (1 sp.), *Mourecotelles* (2 spp.) and *Xanthocotelles* (5 spp.)—the closest relatives of *Colletes* (Michener, 1989, 2007; Kuhlmann et al., 2009). The generic classification of Colletinae follows Toro and Cabezas (1977, 1978) in which *Hemicotelles* and *Xanthocotelles* are considered at the generic level (as opposed to subgenera of *Mourecotelles*; as in Michener, 2007) and *Rhynchocolletes* Moure is a junior synonym of *Colletes* (as opposed to the senior synonym of *Mourecotelles*; as in Moure et al., 2007, 2012). Finally, one stenotritid was sampled to root the trees given that Stenotritidae is the sister taxon of Colletidae (McGinley, 1980; Danforth et al., 2006a, 2006b; Almeida and Danforth, 2009; Almeida et al., 2012, 2019; Branstetter et al., 2017; Sann et al., 2018). Among the sampled *Colletes*, 74 species are from the New World (NW) resulting in the most comprehensive sampling of NW fauna of the genus assembled by a phylogenetic study to date. Of these, 30 species are from the Nearctic and represent 13 of the 18 species groups proposed by Stephen (1954) for North America (the single representative of the *C. impunctatus* Nylander group actually belongs in the *C. clypearis* Morawitz group from the Palearctic; see Kuhlmann et al., 2009). The other 44 species are from the Neotropics, the only biogeographic realm for which the *Colletes* fauna has not been subdivided into either subgenera or species groups (except for *Ptilopoda*, now with two species). With regards to the Old World (OW) *Colletes*, we included 38 species ensuring that all major clades recovered in Kuhlmann et al.'s (2009) phylogeny were well represented in our analyses. All subgenera, including *Rhynchocolletes* which was not sampled by those authors, as well as 30 of the 40 species groups that have been proposed for the OW *Colletes* to date (Noskiewicz, 1936; Kuhlmann et al., 2009; Kuhlmann, 2014b) were included.

The locality, taxonomic and repository information of all studied specimens are listed in Table S2. Most were collected by us, however, some were either borrowed from museums or donated by collaborators (listed in Acknowledgements). The Neotropical Colletinae were identified by the senior author (RF) either with the available keys (Cockerell, 1913, 1914; Toro and Cabezas, 1977, 1978; Genaro, 2003; Ferrari and Silveira, 2015; Balboa et al., 2017; Ferrari, 2017, 2019) and/or with comparison with the primary type specimens. The Nearctic *Colletes*

were initially identified by one of the junior authors (TO), and later confirmed by RF, with the original descriptions and available keys (Stephen, 1954; Mitchell, 1960; Ascher and Pickering, 2019). All OW *Colletes* were identified by an expert on the genus (M. Kuhlmann, Kiel University), except for a few species which were identified by RF with the keys for the Western European (Proshchalykin and Kuhlmann, 2012; Kuhlmann and Proshchalykin, 2014b) and Afrotropical (Kuhlmann and Pauly, 2013) fauna. Most identifications were subsequently confirmed through DNA barcoding (Tables S1 and S3).

### ***Gene locus selection***

The dataset used in our phylogenetic analysis consisted of fragments of four nuclear protein-coding genes (elongation factor-1 $\alpha$  copy F2 [EF1a], long-wavelength rhodopsin [opsin], RNA polymerase II [pol II], and *wingless*) as well as one mitochondrial protein-coding gene (cytochrome c oxidase subunit 1 [COI]—the DNA barcode region), and one nuclear ribosomal RNA locus (28S rRNA large subunit [28S]). A combination of these loci has been extensively employed in molecular phylogenies of bees over the past two decades (*e.g.* Leys et al., 2002; Brady and Danforth, 2004; Danforth et al., 2004, 2006a, 2006b, 2008; Brady et al., 2006, 2011; Larkin et al., 2006; Cameron et al., 2007; Almeida et al., 2008, 2012, 2019; Kawakita et al., 2008; Praz et al., 2008; Almeida and Danforth, 2009; Cardinal et al., 2010; Flores-Prado et al., 2010; Rasmussen and Cameron, 2010; Litman et al., 2011, 2016; Payne, 2014; Praz and Packer, 2014; Martins and Melo, 2016; Trunz et al., 2016), including *Colletes* (Kuhlmann et al., 2009).

Given that the vast majority of the currently available DNA data for *Colletes* had been obtained from OW species (see Kuhlmann et al., 2009), we focused our efforts on sequencing as many NW species of the genus as possible. In total, we sequenced 63 NW *Colletes* species for at least five of our six targeted genes (Table S1). Additional Colletinae for which a full (or nearly so) dataset was available included eight OW species of *Colletes* and eight species from among the other three genera of the subfamily (Table S1). The xeromelissine *Chilicola longiceps* (Ashmead) which belongs in the same subgenus (*Hylaeosoma* Ashmead) as the only two known colletid fossils—*Ch. gracilis* Michener and Poinar and *Ch. electrodominica* Engel (Michener and Poinar, 1996; Engel, 1999; Miklasevskaja, 2017) was also sequenced. Most barcodes used in our analyses are new (see Table S3); the remainder have either been published in a recent taxonomic



revision of the *Colletes* species found in Eastern South America (Ferrari, 2019) or will be published soon in a comprehensive phylogenetic study of the cuckoo-bee genus *Epeolus* Latreille (Hymenoptera: Apidae; Onuferko, 2018). Data for all other outgroups and OW species of *Colletes* were obtained from GenBank. While sequences of all loci were available for nearly all outgroups, only COI and 28S sequences were available for most OW *Colletes*. Sequences of three South American species of *Colletes*—*C. bicolor* Smith, *C. furfuraceus* Holmberg and *C. sp. 1*—were also obtained from GenBank (see Table S1).

To augment our taxon sampling for Neotropical *Colletes*, we added DNA barcodes of 15 species from the following countries: Argentina (1 sp.), Brazil (2 spp.), Costa Rica (2 spp.), Cuba (1 sp.), Mexico (8 spp.) and Nicaragua (1 sp.). The use of DNA barcodes to maximize the representability of highly diverse genera in molecular phylogenies has recently been shown to yield useful results (*e.g.* Trunz et al., 2016; Onuferko, 2018). Due to lack of revisions and keys, we could not confirm the species-level identities of these 15 taxa. All previously obtained DNA barcodes available through collaborators (see Acknowledgements) and new DNA barcode sequences were generated at the Canadian Centre for DNA Barcoding (CCDB) at the University of Guelph (Ontario, Canada). In the case of the species barcoded by us, the right midleg of specimens was removed with flame-sterilized forceps, placed in 96-well plates containing absolute ethanol, and then stored in a -20°C freezer until they were sent to CCDB for processing. Resulting DNA barcodes were uploaded to the Barcode of Life Data System (BOLD) online database (Ratnasingham and Herbert, 2007), where their trace files were inspected for quality. The list of the species for which DNA barcodes were obtained from BOLD and the primer sequences used in the amplifications are in Table S3 and Table S4, respectively.

### ***DNA extraction, amplification and sequencing***

The bee specimens from which we extracted DNA were killed in the field, and then stored, in individual scintillation vials containing absolute ethanol. These were then kept in a -20°C freezer until the specimens were further processed. In most cases, muscle tissue was obtained by grinding the entire specimen's mesosoma with a polypropylene pellet pestle after immersing both in liquid nitrogen within an Eppendorf tube. To permit subsequent morphological analysis of rare specimens, we detached their head, prosternum, propleura and

forelegs and then removed as much muscle tissue as possible from the inside of the exposed mesosomal cavity using extrafine forceps that had previously been flame sterilized; the obtained tissue was then ground as above. Total DNA was extracted using a Mag-Bind® Blood DNA HDQ 96 Kit in Amro Zayed's laboratory at York University as follows. First, 20 µL of Proteinase K Solution and 350 µL of TL buffer were added to each Eppendorf tube, which was then vortexed for 10 minutes and incubated overnight at 50°C. Next, the tubes were centrifuged for 10 minutes (4000 rpm) and the lysates transferred to a new set of tubes which were then centrifuged for another 10 minutes (4000 rpm). The supernatant (*c.* 250 µL) of each tube was transferred to a 96-well microtiter plate, each well of which contained 400 µL of HDQ Binding buffer, 290 µL of AL buffer, and 20 µL of Mag-Bind® Particles HDQ. Another four separate microtiter plates were prepared, the wells of which containing the following reagents: 600 µL of SPM Wash buffer (one plate), 600 µL of VHB buffer (two plates), and 500 µL of nuclease-free water (one plate). A 96-well microplate with 100 µL of elution buffer within each well was also prepared. Finally, all six plates along with a KingFisher 96 KF plate Tip Pick Up were mounted in a KingFisher Flex Magnetic Particle Processor where the automated extraction was performed using the program Thermo Scientific BindIt v.3.3.1. Final solutions containing the extracted DNA were stored in labelled Eppendorf tubes at -20°C until further processing.

The fragments of the five nuclear loci were amplified with the following primers and PCR conditions (all with 35 cycles): 28S – Bel28S-For (Belshaw and Quicke, 1997) and 28SD4-Rev (Danforth et al., 2006a), 94°C for 2 minutes, 58°C for 1 minute, and 72°C for 1.5 minutes; EF1a – HaF2For1 and F2-rev1 (Danforth et al., 1999), 94°C for 1 minute, 54°C for 1 minute, and 72°C for 1.5 minutes; opsin – Opsin-For and Opsin-Rev (Mardulyn and Whitfield, 1999), 94°C for 1 minute, 57°C for 1 minute, and 72°C for 1 minute; pol II – polfor2a and polrev2a (Danforth et al., 2006a), 94°C for 1 minute, 57°C for 1 minute, and 72°C for 1 minute; *wingless* – Wg-Collet-For (Almeida and Danforth, 2009) and Lep-Wg2a-Rev (Brower and DeSalle, 1998), 94°C for 1 minute, 55°C for 1 minute, and 72°C for 1 minute. The primer sequences are listed in Table S4. For all reactions, we prepared a mixture consisting of 28.5 µL of Taq 2× Master Mix, 22.5 µL of double-distilled water, 3 µL of each primer in 10 µM TE buffer, and 3 µL of DNA in elution buffer, totaling 60 µL per sample. We assessed the quality of the crude PCR products by running 5 µL of each sample in agarose-gel electrophoresis. Good-quality, PCR products were sent to Bio Basic Inc. where they were purified and then sequenced.

### ***Sequence assembly and alignment***

The resulting two strands of each sequenced sample were assembled into single sequences in Sequencer v.5 using the default parameters of the automatic assembling option (Dirty data, with ReAligner, 3' gap placement: minimum overlap 20, minimum match 85%). Final sequences were then exported to Mega v.5.2.2 (Tamura et al., 2011) where they were aligned with the algorithm Muscle v.3.3.2 (Edgar, 2004) using the default parameters (gap open - 400, gap extend 0, lambda 24). This procedure was done for each gene separately. We trimmed the longest sequence(s) within each single-locus block to eliminate regions that were poorly represented (*i.e.* present in fewer than half of the sampled taxa). In particular, the sequences of the outgroup species obtained from GenBank were often longer than those generated by us. Regions of 28S where the alignment was highly problematic were also discarded. The boundaries between exons and intron(s) of EF1a (one intron) and opsin (two introns) were assessed by comparing our sequences with those of *Apis mellifera* Linnaeus (Danforth et al., 2006a, b). The introns of the opsin sequences of the outgroups (non-*Colletes* Colletinae excepted) could not be satisfactorily aligned and were also discarded. Last, the nucleotide sequences were translated into peptide sequences to establish correct reading frames and ensure the absence of stop codons. The final length of each single-locus sequence was as follows: 28S (1266 bp), COI (657 bp), EF1a (1004 bp), opsin (667 bp), pol II (811 bp) and *wingless* (419 bp) for a total of 4824 bp.

### ***Data partitioning and phylogenetic methods***

First, each single-locus matrix was individually exported to Mesquite v.3.6 (Maddison and Maddison, 2018) where they were converted into appropriate CFG files for subsequent analyses. The best partitioning scheme and model of DNA evolution was selected for each locus using PartitionFinder v.2.1.1 based on the Bayesian Information Criterion (BIC) using the 'greedy' algorithm (Lanfear et al., 2016). The partitions and respective models determined for each single-locus matrix were as follows: 28S – not partitioned (SYM +  $\Gamma$  + I); COI – 1st and 2nd positions (GTR +  $\Gamma$  + I), 3rd positions (HKY +  $\Gamma$  + I); EF1a – 1st and 2nd positions of exons, 3rd positions of exons, intron (HKY +  $\Gamma$  + I); opsin – 1st and 2nd positions of exons, 3rd

positions of exons, introns (K80 +  $\Gamma$  + I); pol II – 1st and 2nd positions, 3rd positions (HKY + G); *wingless* – 1st and 2nd positions, 3rd positions (GTR +  $\Gamma$  + I).

Single-locus trees were then estimated through Bayesian phylogenetic analyses with the models indicated above. All analyses were conducted remotely in the CIPRES Science Gateway v.3.3 (Miller et al., 2010) using MrBayes v.3.2.6 (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2012). The number of species included in each analysis varied from 73 (pol II) to 130 (COI) according to availability of data. We performed two independent MCMC runs (each containing four chains) for  $5 \times 10^7$  generations, sampling trees and model parameters every  $10^3$  generations. The samples obtained during the initial  $5 \times 10^6$  generations (10%) were discarded as burn-in. Convergence of the two runs, stationarity of the model parameters and length of burn-in were assessed in Tracer v.1.7.1 (Rambaut et. al, 2018a, b). Additional convergence diagnostics included the standard deviation of split frequencies (threshold  $10^{-2}$ ), minimal estimated sample sizes (threshold  $10^4$ ) and potential scale reduction factor (equal or very close to 1). Trees were visualized and edited in FigTree v.1.4.4 (Rambaut, 2016). Support for the clades indicated in the trees was represented by their posterior probabilities which, in turn, were calculated as the percentage of times a given clade was recovered amongst the trees sampled during the post-burnin phase.

We also investigated the evolutionary history of *Colletes* by performing multilocus phylogenetic analyses. The individual single-locus matrices were concatenated into a single matrix, which contained 4824 bp, while maintaining the 13 partitions (and corresponding models of DNA evolution) that had previously been indicated by PartitionFinder. A multilocus Bayesian tree was then estimated in MrBayes following the aforementioned phylogenetic methods.

### ***Divergence time estimation***

A dated multilocus phylogeny for the sampled taxa was estimated in a Bayesian framework, using an uncorrelated lognormal relaxed clock model (Drummond et al., 2006) in BEAST v.2.5.2 (Bouckaert et al., 2014). This analysis was also conducted remotely in CIPRES. First, the multilocus matrix was imported in BEAUti v.2.5.2 (Bouckaert et al., 2014) where the best suitable substitution model for each partition was determined with the ‘BEAST Model Test’ package. Substitution models were unlinked across partitions, whereas the tree estimation and

clock model were linked (see Drummond et al., 2015). The ‘Calibrated Yule Model’ with a random starting tree was defined as the tree prior, and a single calibration point was used to time-calibrate the tree. Specifically, a lognormal distribution (log[mean] 3.4, log[SD] 0.247 [which corresponds to a 95% quantile of 45 Mya, with a median value of 30 Mya]) was assigned to the most recent common ancestor of *Ch. longiceps* and *Ch. rostrata* (Friese), based on the estimated age of the fossil species *Ch. gracilis* and *Ch. electrodominica* from Miocene amber (Michener and Poinar, 1996; Engel, 1999). BEAST was run for  $10^8$  generations, with sampling occurring every  $10^3$  generations. Resulting trace files were imported into Tracer to check convergence, stationarity and the appropriate burn-in. After discarding the trees sampled during the burn-in phase (10%), a maximum credibility clade (MCC) tree was generated in TreeAnnotator v.2.5.2 using common ancestor heights (Drummond et al., 2012). The resulting MCC tree was then visualized, and edited, in FigTree.

### ***Biogeographic analysis***

We investigated the historical biogeography of *Colletes* by reconstructing ancestral geographic ranges for all internal nodes of the ingroup. This approach allowed us to infer the events (vicariance, geodispersal) that best explains the current distribution of *Colletes* globally. To accomplish this, two commonly-used methods for biogeographic inference were explored: the parsimony-based dispersal-vicariance analysis (DIVA; Ronquist, 1997), and likelihood-based dispersal-extinction-cladogenesis (DEC; Ree et al., 2005; Ree and Smith, 2008) model. Both DIVA and DEC analyses were carried out in RASP v.4.1 (Yu et al., 2015) using the package BioGeoBEARS (Matzke, 2013). In fact, BioGeoBEARS implements DIVALIKE which is a likelihood-based approach to DIVA (Matzke, 2013). The adequacy of each model regarding our data was assessed through the likelihood-ratio test implemented in BioGeoBEARS (Yu et al., 2015). Because both DEC and DIVALIKE are based on a common, likelihood framework their reconstructions can be compared pair-wisely (Matzke, 2013, 2014). Ancestral ranges were plotted onto the MCC tree obtained from the BEAST analysis. The following five biogeographic areas were recognized: (A) Neotropical, (B) Nearctic, (C) Palearctic, (D) Afrotropical and (E) Indo-Malaysian. These areas correspond to the biogeographic realms defined by Olson et al. (2001: see Fig. 1); Australasian and Antarctic realms were not considered as *Colletes* occurs in

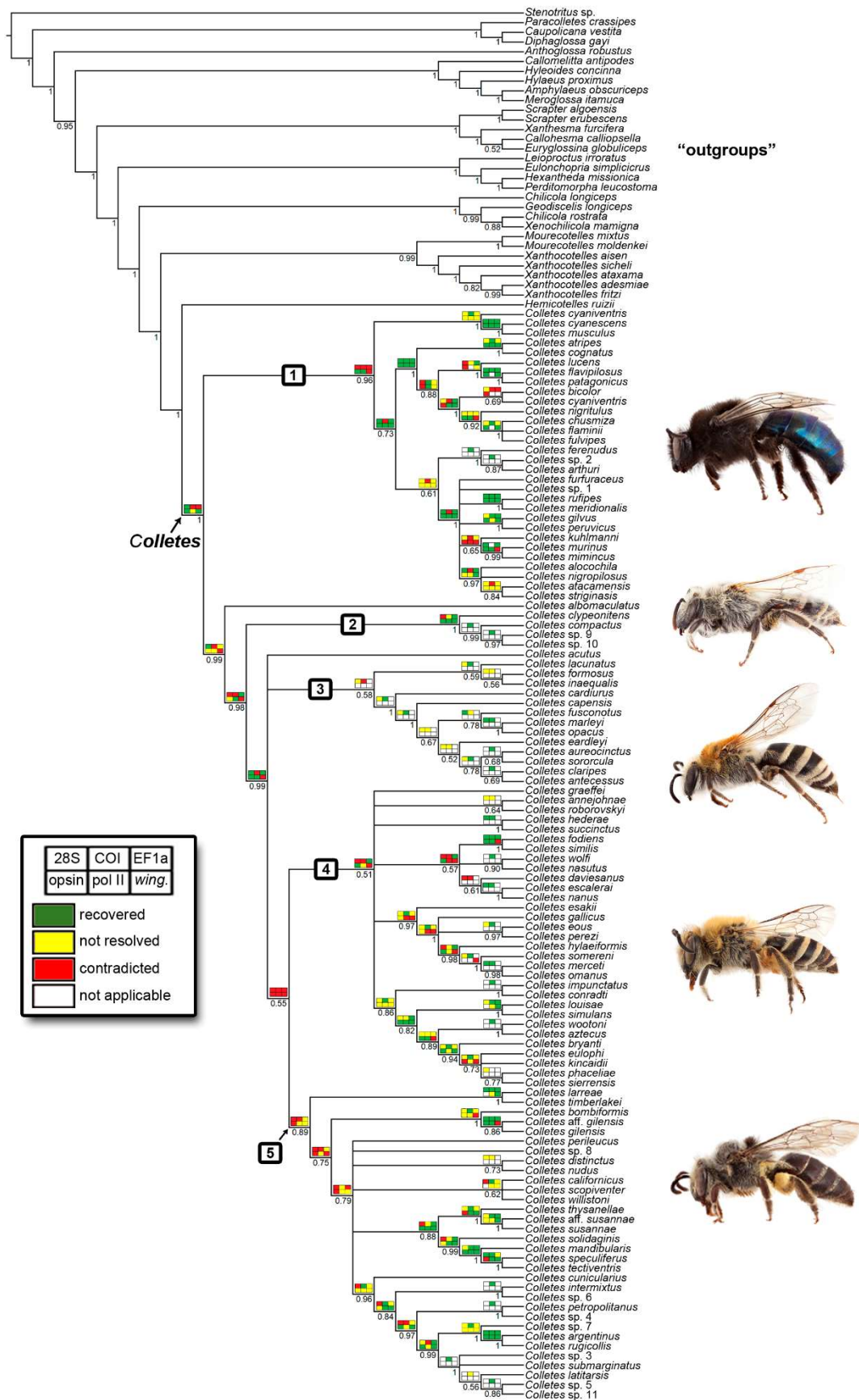
neither. The sources of the geographic data for the Colletinae were threefold: (i) comprehensive online databases on bees (Moure et al., 2012; Ascher and Pickering, 2019), (ii) senior author's personal database which was compiled for the purpose of taxonomic revisions of South American *Colletes* (Ferrari and Silveira, 2015; Ferrari, 2017, 2019); and (iii) discussions with an expert on OW *Colletes* (M. Kuhlmann, *pers. comm.*). We constrained the analyses to allow no ancestral species to occupy more than two areas (as in Voelker, 1999; Praz and Packer, 2014; Trunz et al., 2016). Unrealistic ranges (*e.g.* Nearctic and Indo-Malay) were excluded, and probabilities were set to 1.0 for geodispersal among adjacent areas (*e.g.* Palaearctic and Indo-Malay).

## Results

### *Power of resolution and phylogenetic signal of different loci*

Our results showed that the power of resolution of each of the six single-locus analyses (Figs. S1–S6) was relatively low, even though support for the retrieved clades was moderate to strong overall—the proportion of highly-supported clades (PP 90–100) varied between 53–68% among analyses. While opsin yielded the most resolved tree (Fig. S4) which contained roughly 81% of the maximum possible number of internal nodes (68 of 84), the analysis of 28S resulted in a largely unresolved tree (Fig. S1) with merely 49% of the maximum possible number of internal nodes being recovered (59 of 120; note that the denominator depended on the number of taxa for which sequences were available). The analyses of the other four loci yielded intermediate results (see Figs. S2, S3, S5 and S6). In general, the nuclear protein-coding genes and 28S were very efficient at resolving the deeper relationships (including those among the outgroups), whereas COI resolved mostly the shallower ones.





**Fig. 1.** Bayesian tree obtained through analysis of the multilocus dataset matrix in MrBayes. Phylogenetic signal of, and topological congruence between, each individual locus with respect to the multilocus analysis are depicted according to the colour codes shown in the box on the left. ‘Not applicable’ means that topological congruence could not be assessed because taxon sampling for the corresponding locus was insufficient. Numbers below internal branches are posterior probabilities of the clades retrieved in the multilocus analysis. Boxed numbers from 1–5 indicate the five major clades of *Colletes*. Exemplars illustrating some of the diversity of *Colletes* are: female *C. cyaniventris* (clade 1), female *C. clypeonitens* (clade 2), female *C. zuluensis* (clade 3), female *C. halophilus* (clade 4) and female *C. petropolitanus* (clade 5).

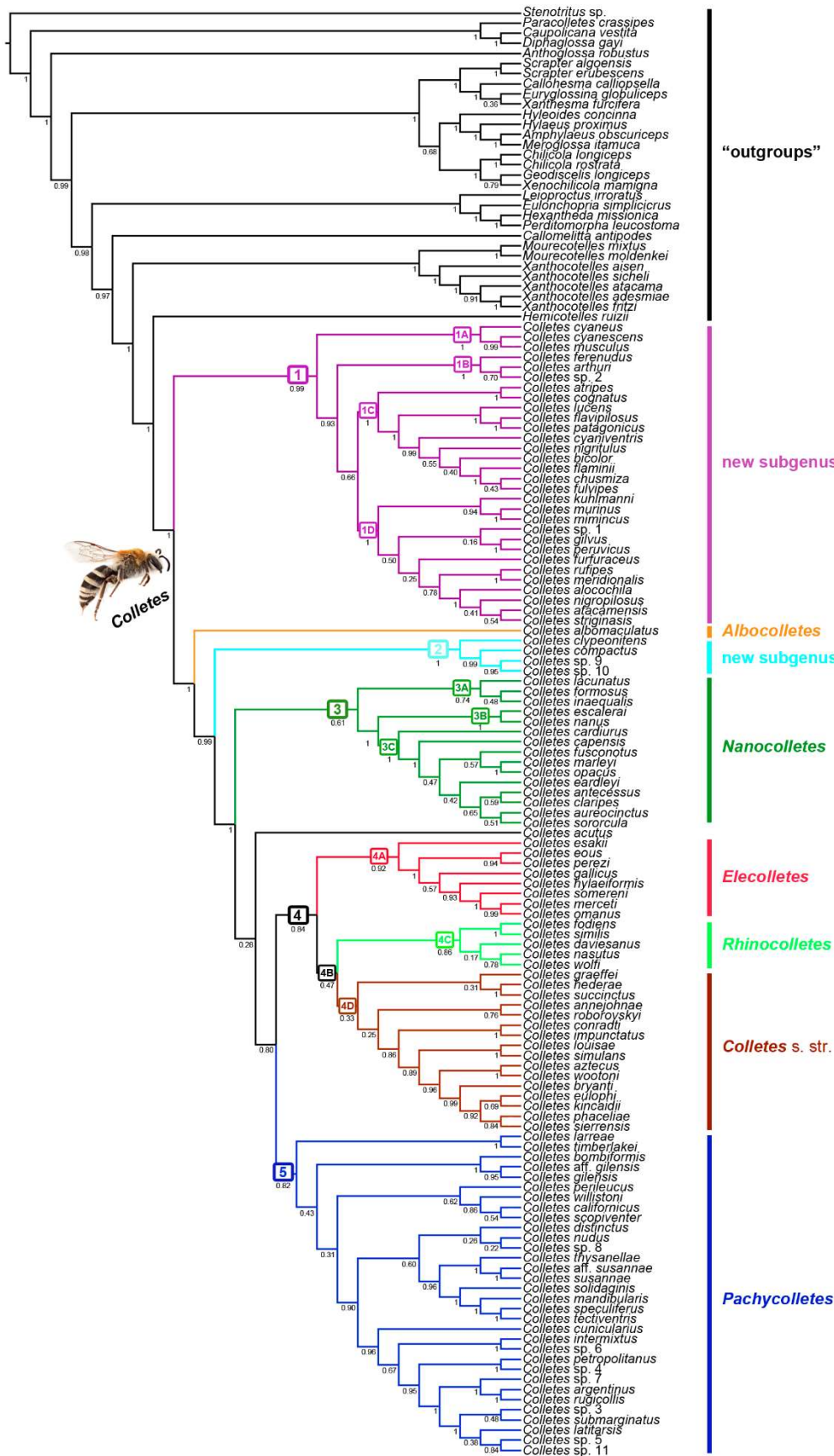
Overall, the phylogenetic signal of the single-locus datasets was incongruent among loci (Fig. 1). COI (Fig. S1) and 28S (Fig. S2) yielded the most contradictory topologies in comparison to the one resulting from the multilocus analysis (Fig. 1), although it should be noted that these were the only data available for *c.* 35% of the sampled species (Table S1). In turn, the phylogenetic signal of both EF1a and pol II were largely congruent with that of the multilocus dataset (Fig. 1; see also Figs. S3 and S5, respectively). However, an important exception to the aforementioned patterns is noteworthy: while *Colletes* was recovered as monophyletic with maximum support in both analyses of 28S (Fig. S1) and the multilocus dataset (Fig. 1), its monophyly was contradicted by the analysis of EF1a (Fig. S3). In the latter, *Hemicotelles ruizii* (Herbst) was recovered as the sister species of *C. cyanescens* (Haliday) plus *C. musculus* Friese suggesting paraphyly of *Colletes* (Fig. S3). Additionally, the analysis of COI placed the species of *Mourecotelles* within a large polytomy which contained the bulk of the species of *Colletes*, thus also rendering the latter paraphyletic (Fig. S2). However, while analysis of pol II (Fig. S5) was inconclusive, *Colletes* was recovered as a strongly-supported, monophyletic group in analyses of both opsin (Fig. S4) and *wingless* (Fig. S6).

### ***Multilocus analyses***

The Bayesian phylogenetic analyses conducted with the multilocus dataset in MrBayes and BEAST resulted in trees of very similar topologies (Fig. 1 and Fig. 2, respectively). Nevertheless, we present the results of the latter because it was fully resolved and therefore conveyed more information regarding the relationships at both deep and shallow nodes (see Fig. 2). The monophyly of *Colletes*, as well as its sister-group relationship to *Hemicotelles*, were retrieved with maximum support. Together, the two genera were placed as sister to the clade

containing *Mourecotelles* and *Xanthocotelles* which, in turn, were also recovered as reciprocally monophyletic with maximum support (Fig. 2).

The phylogenetic tree of *Colletes* (Fig. 2) consists of five major clades and two isolated single species lineages, as follows. A strongly-supported clade (clade 1) containing exclusively South American species was recovered as the sister group to the remaining *Colletes*. Clade 1 encompassed four subclades (clades 1A–1D) each of which were retrieved with maximum support. None belong to any of the previously described subgenera of *Colletes*. A second, small clade (clade 2) was recovered with maximum support and included four species from the Nearctic/Northern Neotropics: two of them—*C. clypeonitens* Swenk and *C. compactus* Cresson—remain unplaced to subgenus at present (the identity of the other two could not be determined). A third clade (clade 3), weakly-supported, consisted of three members of *Pachycolletes* (clade 3A), all sampled *Nanocolletes* (clade 3B) and all but one of the included Afrotropical species (clade 3C) that belong in none of the currently available subgenera. While clade 3A was relatively weakly supported, clades 3B and 3C as well as the sister-group relationship between the two were recovered with maximum support. A fourth, relatively weakly supported clade (clade 4) included species from a range of named subgenera. Clade 4A was well supported and included all species of *Elecolletes* in our analysis. It was placed as sister to a weakly-supported clade (clade 4B) which included, among others, the type species of four different available subgenera: *C. graeffei* Alfken (*Denticolletes*), *C. nasutus* Smith (*Rhinocolletes*), *C. succinctus* (Latreille) (*Colletes* s. str.) and *C. similis* Schenk (*Simcolletes*). Within clade 4B, the species of the *C. similis* group formed a monophyletic group with *C. nasutus* and *C. wolffi* Kuhlmann (clade 4C) without the remaining species of *Simcolletes* (which were placed in clade 4D). The fifth clade (clade 5), which was recovered with moderate support, consisted solely of NW *Colletes*, except that it included *C. cunicularius* (Linnaeus) a widespread species in the Palaearctic. While the bulk of species included in clade 5 remain unplaced in subgenera, a number of them belong in *Pachycolletes*. *Colletes albomaculatus* (Lucas) is an isolated taxon in the phylogeny—the type species of the subgenus *Albomaculatus*. *Colletes albomaculatus* was recovered as the sister species of all *Colletes* excluding those of clade 1 with maximum support. The second isolated branch corresponds to *C. acutus* Pérez which was recovered as sister to clade 4 plus clade 5; however, this relationship was very weakly supported.



**Fig. 2.** Maximum clade credibility tree inferred through Bayesian analysis of the multilocus dataset matrix in BEAST. Colour-coded, vertical bars on the right depict the intrageneric classification of *Colletes* proposed in this paper. Numbers below internal branches are posterior probabilities of the corresponding clades. Boxed numbers from 1–5 show the five major clades of *Colletes*; boxes with numbers followed by letters indicate other clades of relevance mentioned in the text. Exemplar at the node of *Colletes* is a female *C. zuluensis*.

### ***Divergence time estimates and historical biogeography***

Our dating analysis in BEAST (Figs. 3 and S7) indicated that the most recent common ancestor (MRCA) of Colletinae arose near the early-middle Eocene boundary (stem age 47.7 Mya, 95% highest probability density [HPD] 77.6–23.3 Mya). The extant colletines, however, likely began diversifying only in the late Eocene (crown age 36.1 Mya, 95% HPD 59.2–16.8 Mya). The analysis also indicated that *Colletes* and *Hemicotelles* probably diverged from one another in the early Oligocene (stem age 32.8 Mya, 95% HPD 53.2–14.8 Mya), and that the diversification of extant *Colletes* may have begun in the late Oligocene (crown age 27.4 Mya, 95% HPD 45.1–12.3 Mya). The crown ages of all five major clades of *Colletes* (clades 1–5) date to the middle Miocene (15.5–13.9 Mya), except the South American clade 1, the crown age of which was placed in the late Oligocene (24.4 Mya, 95% HPD 40.8–11.7 Mya).

The model test analysis conducted with BioGeoBEARS in RASP indicated that the DEC model, without the founder-event speciation parameter ( $j$ —Matzke, 2014), was the one that best suited our data (LnL -106.6). In comparison, the DIVALIKE model (Fig. S8) was more weakly supported by the same analysis (LnL -117.2) and consequently we mention only the former in detail (but see the Discussion). The DEC analysis (Fig. 3a) inferred that the MRCA of *Colletes* probably had a Pan-American distribution (*i.e.* its geographic range included both the Neotropics and Nearctic) during the late Oligocene (crown age 27.4 Mya). The probability of this ancestral range reconstruction based on our data was 98.5%. In total, six lineage interchanges between the two realms were suggested (Fig. 3b): two geodispersal events from the Neotropics to the Nearctic (crown ages 27.4 and 4.7 Mya), and four events in the opposite direction (crown ages 10.7, 10.3, 6.6 and 6.2 Mya). The DEC analysis also inferred that *Colletes* first colonized the Palaearctic from the Nearctic likely during the late Oligocene (crown age 23.9 Mya). There were two additional geodispersal events each from the Nearctic into the Palaearctic (crown ages 11.4

and 1.9 Mya) and from the latter to the former (crown ages 10.1 and 10.0 Mya). From the Palearctic, *Colletes* spread into the Afrotropics twice, once in the middle Miocene (crown age 12.6 Mya) and then in the latest Miocene (crown age 5.5 Mya); none was inferred as occurring in the opposite direction (Fig. 3b). The Indo-Malay was probably the last realm to be colonized by *Colletes*; however, we could not verify when this event occurred because no ancestral range including this realm was reconstructed: rather two Palearctic species have extended their range into the Indo-Malay (Fig. 3b).

## Discussion

### *Phylogenetic analyses*

In this paper, we provided the most comprehensive molecular phylogeny of *Colletes* to date; comprehensive both in terms of number of species included (112 spp., >20% of the known total) and the amount of data employed (six loci, 4824 bp) in the analyses. In particular, we performed a dense taxon sampling regarding the NW fauna of the genus (74 spp., c. 66% of the total) which allowed us to shed light on the largely unknown relationships among these lineages for the first time. Both phylogenetic analyses conducted with the multilocus dataset matrix yielded very similar topologies (Figs. 1 and 2), in which five major clades and two isolated species were retrieved. Overall, support for these clades varied from weak (*e.g.* clade 3, posterior probability [PP] 0.58–0.61) to maximum (*e.g.* clade 2). Some less inclusive clades, most notably those within clades 4 and 5, were composed of relatively long terminal branches connected by short internodes (Fig. S7) which likely explained, at least partially, their weak support (for a detailed discussion on the topic, see Alfaro et al., 2003).

Analyzing each single-locus dataset separately (Figs. S1–S6) allowed us both to assess their individual power of resolution and to compare the congruence between their phylogenetic signal with that of the multilocus dataset (Fig. 1). Our results showed that both parameters were low overall, with the exception of the power of resolution of opsin (Fig. S4) and the congruence between the phylogenetic signals of pol II (Fig. S5) and the multilocus dataset which were relatively high (Fig. 1). In the analysis of COI (Fig. S2), *Mourecotelles* rendered *Colletes* paraphyletic, a result that had previously been reported by Kuhlmann et al. (2009). It has been



demonstrated that mitochondrial genes tend to show both greater base compositional bias and higher rates of substitutions in comparison with nuclear genes (Timmermans et al., 2015), which often lead to higher levels of homoplasy (Kjer et al., 2001; Lin and Danforth, 2004). As a result, mitochondrial genes are usually more prone to yield spurious trees if analyzed alone (Lee, 2009; Kjer et al., 2014; Trunz et al., 2016). It is important to point out that *Colletes* was also recovered as paraphyletic in the analysis of one of the nuclear loci sampled by us—EF1a (Fig. S3). A previous phylogenetic study on bees showed that the base composition of EF1a may be remarkably heterogeneous among taxa and concluded that such heterogeneity may profoundly impact phylogenetic reconstructions (Praz and Packer, 2014). Nevertheless, the monophyly of *Colletes* was highly supported by our preferred multilocus analyses (Figs. 1 and 2) which confirmed an historical understanding that had been constructed based on morphological grounds (Michener 1989, 2007; see also Chapter 2). A series of clades recovered within *Colletes* by the multilocus analysis was supported by none of the individual loci (*i.e.* hidden support; see Gatesy et al., 1999; Lee, 2009; Gatesy and Springer, 2014). Perhaps our most illustrative example of hidden support was the node uniting clades 4 and 5 which was contradicted by all six single-locus analyses (Fig. 1; see also Figs. S1–S6). This result alone indicates the unpredictable nature of analyses of concatenated sequences even when the phylogenetic signals of their constituent partitions are known (reviewed by Degnan and Rosenberg, 2009).

It appears safe to assume that our phylogenetic analyses were, at least to some extent, negatively affected by the significant amount of missing data (sometimes also referred to as ‘incomplete taxa’; see Kearney, 2002; Wiens, 2003) contained in our multilocus matrix. Of the 112 *Colletes* species sampled by us, only 61 (*c.* 54%) were sequenced for the nuclear protein-coding genes (EF1a, opsin, pol II, *wingless*) employed in the analyses (see Table 1). The reasons for the missing data regarding the other 51 species were twofold: first, only 28S and COI data were available for 30 of the 38 OW species of *Colletes*, all of them originally sequenced by Kuhlmann et al. (2009), except *C. nasutus* (Schmidt et al., 2015). Perhaps this is why clades 3 and 4, in which nearly all OW *Colletes* were nested, were recovered with weak (PP 0.61) and moderate (PP 0.84) support, respectively (Fig. 2). Another explanation would be that both clades 3 and 4 are actually not monophyletic and that the missing data associated with their constituent taxa contributed to the recovery of a spurious topology. Second, we adopted an approach of using DNA barcodes to augment our taxon sampling, as Trunz et al. (2016) did with regards to

the Megachilini. If on the one hand this approach allowed us to include a series of Neotropical species from otherwise poorly-sampled regions (mostly notably tropical Mexico, see Tables S1 and S2), on the other it added substantially to the amount of missing data. Nevertheless, the use of DNA barcodes in combination with slowly-evolving nuclear genes resulted in an encouraging phylogeny which permitted us both to propose an updated intrageneric classification for *Colletes* (Fig. 2; refer to section 4.2) and investigate its historical biogeography (Fig. 3; refer to section 4.3).

### ***Intrageneric classification***

Constructing a phylogeny with a comprehensive sampling of the Neotropical *Colletes* permitted us to, for the first time, allocate all species currently accepted as valid in the realm into species groups (Table S5). While the Old World (Noskiewicz, 1936, Kuhlmann et al., 2009; Kuhlmann, 2014b) and Nearctic (Stephen, 1954) faunas of *Colletes* had already been organized into species groups, no study had yet attempted to expand this almost century-old tradition to the Neotropics. All 18 species groups proposed herein include exclusively Neotropical *Colletes*, even though a significant proportion of the species found in this realm actually belong in groups that had originally been described for the Nearctic (Stephen, 1954; see also Table S5). The placement of most species not included in our phylogenetic analyses into the proposed groups was made based on the shape of male S7, which has been widely recognized as the most useful feature for species delimitation and identification within *Colletes* (e.g. Noskiewicz, 1936, Stephen, 1954; Mitchell, 1960; Kuhlmann, 2000; Ferrari, 2017). However, for a number of species (mostly from Argentina, Central America and tropical Mexico) only the original descriptions were available and, therefore, their placement is only tentative (indicated by question marks in Table S5).

The major relationships within *Colletes* (Fig. 2) were considerably different from those reported previously by Kuhlmann et al. (2009), even though a significant proportion of the data used in our phylogenetic analyses had originally been generated by those authors. For example, the early-diverging South American lineages of *Colletes* formed a strongly-supported monophyletic group (clade 1) in our multilocus analysis (Fig. 2), whereas the ones sampled by Kuhlmann et al. (2009) came out as a series of isolated clades near the MRCA of *Colletes*. Also,

the sampled members of the *C. fodiens* (Fourcroy) group formed a monophyletic group with *C. nasutus* (*Rhinocolletes*) and *C. wolfi* (*Colletes* s. str.) in our analysis (Fig. 2) rather than with the other *Simcolletes* as in Kuhlmann et al.'s (2009) phylogeny. Therefore, we argue that a new intrageneric classification for *Colletes* based on our phylogenetic results appears warranted (Table S6).

### *Clade 1*

Clade 1 is an exclusively South American one which included, as far as we could determine, 66 of the 123 valid species (*c.* 54%) of *Colletes* found on the continent (for an updated checklist, see Table S5). Our results showed that Clade 1 fits in none of the currently available subgenera (Fig. 2) and, therefore, a new subgenus must be described to accommodate its constituent species (Table S6). However, it is important to point out that such a subgenus would encompass a series of clearly-distinct forms found in South America, thus rendering its diagnosability particularly difficult. For example, it would include the large species with metallic-blue metasoma from Central Chile and Western Argentina (*e.g.* the *C. cyaneus* Holmberg group), more typical grey-haired species with pale apical tergal bands (*e.g.* the *C. gilvus* Vachal group) as well as the black small species found in Southern Peru and Northern Chile (*e.g.* the *C. alocochila* Moure group). However, we minimized the proliferation of subgeneric names by putting all these species into one subgenus, although to adequately convey the taxonomic complexity within this lineage, we recommend the use of 14 species groups (Table S5). As argued by Kuhlmann et al. (2009), species groups are informal, yet useful, alternatives to describing large numbers of subgenera which can be redefined whenever further phylogenetic evidence is available. This approach has been adopted in the taxonomy of other species-rich bee genera, such as *Euglossa* Latreille (Dressler, 1978, 1982a, b, c; Roubik, 2004; Ferrari et al., 2017), *Nomada* Scopoli (Alexander, 1994) and *Epeolus* Latreille (Onuferko, 2018). Another possibility would be to describe a new subgenus for each of the four main lineages recovered within clade 1 (*i.e.* clades 1A–1D; see Fig 2). This approach would certainly facilitate their diagnosability, but it would inflate the classification of *Colletes* by erecting multiple subgenera for relatively small group of species (*i.e.* clades 1A and 1B).

## *Colletes albomaculatus*

*Colletes albomaculatus* is the type species of the subgenus *Albocolletes* which also includes another three Palearctic species: *C. alfkeni* Noskiewicz, *C. dorsalis* Morawitz and *C. punctatus* Mocsary (Kuhlmann, 2000), none of which were available for sequencing. In our multilocus analysis, *C. albomaculatus* was recovered as not belonging to any of the five major clades that constituted the phylogenetic tree of *Colletes*; instead it was placed (with maximum support; Fig. 2) as an isolated terminal sister to all of its congeners, except those of clade 1. Thus, the maintenance of the subgeneric status of *Albocolletes* as currently understood (Table S6) is endorsed by the present study.

## Clade 2

Clade 2 is a small, exclusively North American group which fits into none of the currently available subgenera of *Colletes* (Fig. 2). Therefore, a new subgenus to accommodate its constituent species is needed (Table S6). Clade 2 had maximum support and included the Nearctic *C. compactus* and *C. clypeonitens* (the former is the sole member of the *C. compactus* group while the second belongs in the *C. daleae* Cockerell group which contains nine valid species (Stephen, 1954)) as well as two unidentified species from tropical Mexico. In Kuhlmann et al.'s (2009) phylogeny, both *C. compactus* and *C. clypeonitens* were recovered as more closely related to Neotropical *Colletes*, however, they were here shown to be closer to the OW species belonging to clade 3 (Fig. 2).

## Clade 3

Clade 3 consisted of three major monophyletic groups (Fig. 2): one included three of the largest species of *Pachycolletes* (clade 3A), another the representatives of *Nanocolletes* (clade 3B), and the third all Afrotropical species, except *C. somereni* Cockerell (clade 3C). Two main conclusions can be drawn from this finding. Firstly, that *Pachycolletes* is polyphyletic given that the other representatives of the subgenus (including its type species, *C. cunicularius*) were nested within clade 5 (Fig. 2). The status of *Pachycolletes* is discussed below (section 4.2.7; see also

Table S6). Secondly, it was shown that the bulk of the Afrotropical species (for which no subgenus is currently available) constituted the sister group of *Nanocolletes*, as previously indicated by Kuhlmann et al. (2009). Thus, we herein propose that *Nanocolletes* be expanded to include, in addition to the *C. nanus* Friese and *C. foveolaris* Pérez groups (clade 3B), also the *C. inaequalis* Say, *C. formosus* Pérez and *C. lacunatus* Dours groups of *Pachycolletes* (clade 3A), as well as all species groups that have been proposed for the Afrotropical *Colletes* so far (clade 3C; see Table S6). As proposed herein, *Nanocolletes* would include *c.* 100 valid species mainly distributed in the Afrotropics, although the subgenus would also be relatively-well represented in the Holarctic. Two alternatives to our proposal would be to describe a new subgenus for clade 3A while expanding *Nanocolletes* to clade 3C only, or, describing one subgenus each for both clades 3A and 3C while maintaining *Nanocolletes* as it is currently circumscribed (Kuhlmann et al., 2009).

### *Colletes acutus*

The second isolated terminal branch in our tree led to *C. acutus* which with *C. acutiformis* Noskiewicz composes the Palearctic *C. acutus* group (Noskiewicz, 1936; Kuhlmann, 2010). *Colletes acutus* has historically been classified within *Pachycolletes* (Warncke, 1978; Kuhlmann et al., 2009), however, our analysis showed that it actually belongs to none of the currently available subgenera of *Colletes* (Fig. 2). Even though recommending description of a new subgenus to accommodate the members of the *C. acutus* group may appear sensible, the nodal support for the recovered arrangement (*i.e.* *C. acutus* as sister to clade 4 plus clade 5; see Fig. 2) was very weak. Thus, we opted to place both *C. acutus* and *C. acutiformis* as *incertae sedis* (Table S6). More data (particularly from slowly-evolving loci) are needed to verify whether the two species should in fact be included in a yet-to-be described subgenus, or, whether the inferred weak support (which is most likely a result of a very short internode; see Fig. S7) is an indication of a spurious topology.

#### Clade 4

Clade 4 included two subclades: all representatives of *Elecolletes*, which formed a relatively strongly-supported monophyletic group (clade 4A, PP 0.92) and its sister group (*i.e.* clade 4B; Fig. 2). Although the type species of *Elecolletes*, *C. elegans* Noskiewicz, could not be included in our analysis, we did include *C. omanus* Kuhlmann, which is the most probable sister species of *C. elegans* (Kuhlmann et al., 2009). *Elecolletes* is herein circumscribed (Table S6) exactly as it was by Kuhlmann et al. (2009), containing the *C. carinatus* Radoszkowski, *C. caspicus* Morawitz, *C. hylaeiformis* Eversmann, *C. nigricans* Gistel and *C. squamosus* Morawitz groups (Table S6). As per our proposal, all *Elecolletes* species would be confined to the Palearctic, except *C. somereni* (*C. squamosus* group) which is Afrotropical (Kuhlmann, 2010; Ascher and Pickering, 2019).

Classification of clade 4B was particularly challenging as it included the type species of four subgenera. Furthermore, nodal support for its constituent clades was very weak overall which rendered the situation even more complicated (Fig. 2). Within clade 4B, the members of the *C. fodiens* group (including *C. similis*, type species of *Simcolletes*) formed a monophyletic group (clade 4C) with the type and single species of *Rhinocolletes* (*C. nasutus*) but without the remaining species of *Simcolletes* (Fig. 2). Kuhlmann et al (2009) predicted that *C. nasutus* (which was not included in their analysis) would be a close relative to *C. albomaculatus*, presumably based on morphological data. However, none of our analyses confirmed this prediction; instead they showed that *C. albomaculatus* and *C. nasutus* belong to distantly-related lineages within *Colletes* (Figs. 1 and 2). Here, we suggest that *Simcolletes* be synonymized with *Rhinocolletes*; the latter would then include the following Palearctic species groups: *C. nasutus*, *C. anchusae* Noskiewicz (*Colletes* s. str.) and *C. fodiens* (*Simcolletes*) groups, and possibly the *C. senilis* (Eversmann), *C. tardus* Noskiewicz and *C. uralensis* Noskiewicz groups (*Simcolletes*). However, the sister-group relationship between *C. daviesanus* Smith plus *C. nasutus* and *C. wolffi* was very poorly supported (PP 0.17) and, therefore, it would also be sensible to maintain *Simcolletes* as a valid subgenus while expanding *Rhinocolletes* to also include the *C. anchusae* group.

Clade 4D nested the sister species *C. succinctus* and *C. hederæ* Schmidt and Westrich (*Colletes* s. str.) which formed a monophyletic group with the type and single species of



*Denticolletes*, *C. graeffei* (Fig. 2). Together, they were recovered as sister to the clade containing *C. annejohnae* Kuhlmann (*C. mixtus* Radoszkowski group), *C. roborovskyi* Friese (*C. roborovskyi* group) and all species currently classified within *Simcolletes*, except those of the *C. similis* group (see above). Based on this result, we argue that the monotypic *Denticolletes* be synonymized with *Colletes* s. str. Moreover, the latter should also be expanded to include the *C. mixtus* and *C. roborovskyi* groups (currently placed in no subgenus), and the *C. clypearis*, *C. conradti* Noskiewicz, *C. marginatus* Smith and *C. simulans* Cresson groups of *Simcolletes* (Table S6). Alternatively, the status of both *Colletes* s. str. and *Denticolletes* could be maintained as currently established (Kuhlmann et al., 2009; see also Table S6), meaning that a new subgenus would need to be erected for the combination of four species groups currently considered in *Simcolletes*.

#### Clade 5

Clade 5 included the bulk of the sampled *Pachycolletes* (including its type species, the Palearctic *C. cunicularius*) although most of its constituent species are currently placed in none of the available subgenera (Tables S5 and S6). In our preferred tree, *C. cunicularius* was recovered as more closely related to some of the exclusively NW groups of *Colletes* (particularly to the *C. intermixtus* Swenk group) rather than to the Palearctic ones that are currently classified within *Pachycolletes* (i.e. *C. acutus*, *C. formosus* and *C. lacunatus* groups; see Fig. 2 and Table S6). The analysis also showed, for the first time, that various Nearctic groups that were proposed by Stephen (1954) should be considered to belong to *Pachycolletes*, namely: *C. americanus* Cresson, *C. consors* Cresson, *C. hyalinus* Provancher, *C. intermixtus*, *C. latitarsis* Robertson, *C. nudus* Robertson, *C. productus* Robertson, *C. robertsonii* Dalla Torre and *C. willistoni* Robertson groups (Table S6). Moreover, four of the Neotropical species groups proposed herein that are not members of Clade 1—*C. bombiformis* Metz, *C. petropolitanus* Dalla Torre, *C. rugicollis* Friese and *C. spilopterus* Cockerell groups—also belong in *Pachycolletes* according to our phylogenetic results (Table S6).

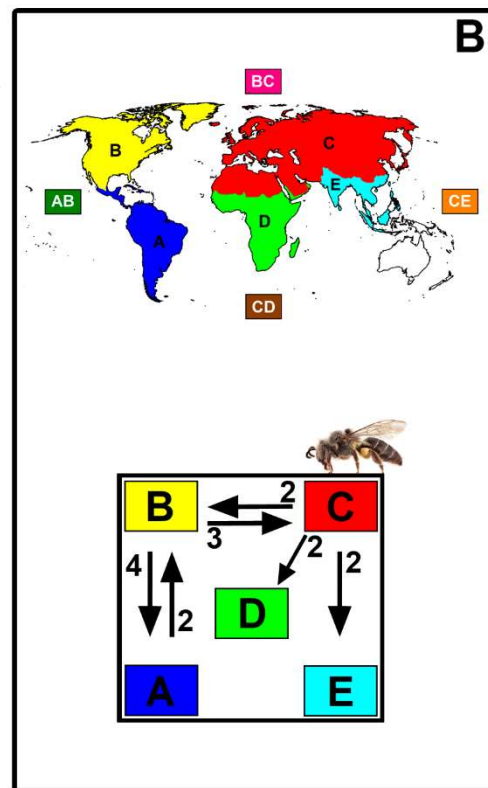
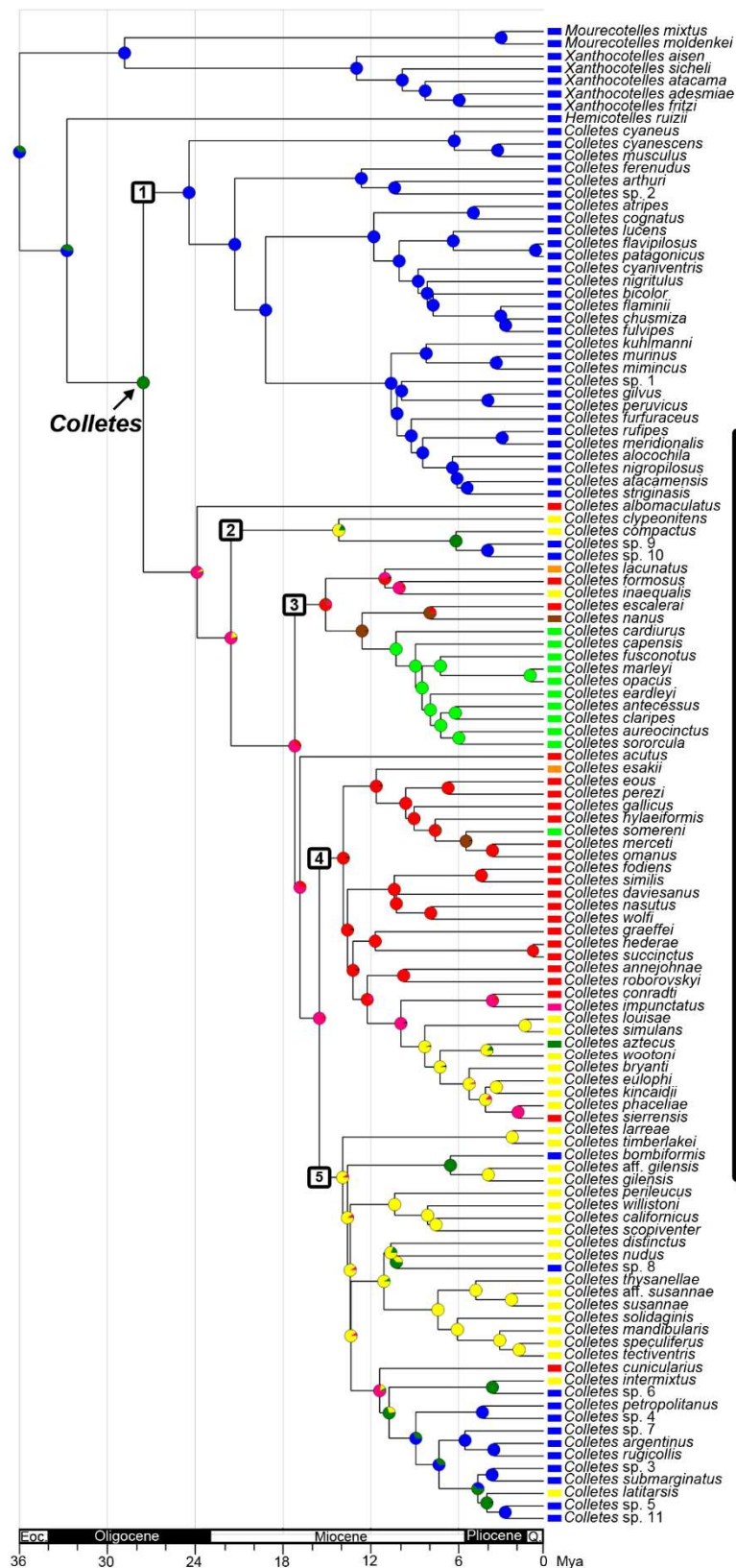
Based on the morphology of the male S7, which is remarkably variable among *Colletes* species, it is likely that the Neotropical *C. spilopterus* Cockerell (the type species of *Ptilopoda*) would have been placed as sister to, or even within, the *C. latitarsis* group had the species been

available and included in our analysis (see Michener, 1954: Fig.1 and Stephen, 1954: Fig. 10). If this conjecture proves correct in a future phylogenetic study, *Pachycolletes* will need to be synonymized under *Ptilopoda*.

### ***Divergence times and historical biogeography***

Our mean divergence time estimates should be interpreted with caution due to the large 95% HPD intervals obtained, especially regarding the earliest-diverging lineages within Colletinae (Fig. S7). The most plausible cause of such outcomes was likely the use of a single calibration point in our dating analysis (Mairal et al., 2017)—the estimated minimum age (45 Mya) of the fossil species *Ch. gracilis* and *Ch. electrodominica* (Michener and Poinar, 1996; Engel, 1999) assigned to the MRCA of *Ch. longiceps* and *Ch. rostrata* (Miklasevskaja, 2017). Whereas the use of secondary calibration points (*i.e.* those estimated by other studies) in phylogenetic reconstructions has been questioned by some authors (*e.g.* Shaul and Graur, 2002; Graur and Martin, 2004; but for a different opinion see Hedges and Kuman, 2004), we opted to rely solely on the fossil record to time-calibrate our phylogeny. Our divergence time estimates were, therefore, likely accurate though imprecise. Nevertheless, the stem and crown ages of *Colletes* estimated herein (*c.* 33 and 27 Mya, respectively) matched very closely those estimated by a previous phylogenetic study on colletid bees (30 and 24 Mya, respectively; Almeida et al., 2012).

Even though we investigated the historical biogeography of *Colletes* using two different models—DEC (Fig. 3) and DIVALIKE (Fig. S8)—the former was indicated by the likelihood-based, model test analysis in BioGeoBEARS as the most suitable for our data (LnL -106.6 vs. -117.2, respectively). We did not incorporate into our DEC analysis the *j* parameter which allows for speciation through long-distance geodispersals (Matzke, 2014) for two reasons. First, such geodispersal events appear very improbable for ground-nesting *Colletes* which usually fly for short distances (Peakall and Schiestl, 2004). Second, Ree and Sanmartín (2018) demonstrated empirically that the DEC+J model may be highly unparsimonious.



**Fig. 3.** Maximum clade credibility chronogram (without outgroups) obtained through dated Bayesian analysis of the multilocus matrix in BEAST. (A) Pie-charts depict ancestral geographic ranges of corresponding nodes inferred by the BioGeoBears analysis under the DEC model in RASP. Boxed numbers from 1–5 indicate the five major clades of *Colletes*. (B) Map illustrating the five biogeographic areas (A–E) considered in the analysis; polymorphic ranges are shown within rectangles. Arrows and corresponding numbers in the diagram below the map represent the lineage exchanges among geographic areas inferred by the DEC model; the bee resting on the diagram is a female *C. petropolitanus*. Eoc = Eocene; Q = Quaternary.

Our preferred DEC analysis indicated that the divergence between *Colletes* and *Hemicotelles* in the early Oligocene (stem age 32.8 Mya) took place somewhere in the Neotropics (Fig. 3a). Whereas both *Hemicotelles* and the earliest-diverging lineage of *Colletes* (clade 1) are confined to South America (Fig. 3a), it is very likely that the two genera diverged within that continent. The fact that their closest relatives (*i.e.* *Mourecotelles* and *Xanthocotelles*) are also South American further supports this hypothesis. A South American origin of *Colletes* has long been suspected (Michener, 1979, 1989, 2007), although it has only recently been supported by phylogenetic evidence (Kuhlmann et al., 2009; Almeida et al., 2012). *Colletes* likely arose at the onset of a major Antarctic glaciation event—the Eocene-Oligocene transition—which resulted from a prolonged period of global cooling initiated in the middle Eocene (Zachos et al., 2001, 2008; Houben et al., 2012; Mudelsee et al., 2014; Pound and Salzmann, 2017). As a consequence, tropical forest that covered South America almost entirely in the Palaeocene began gradually being replaced with *Nothofagus*-dominated forest at high latitudes, and with open-vegetation biomes towards the centre of the continent (Iglesias et al., 2011; Meseguer et al., 2015). The combination of these biotic and abiotic factors likely played an important role in the diversification of the *Colletes* lineages that remained isolated in South America.

The most unexpected result of our DEC analysis was arguably a Pan-American distribution being inferred for the MRCA of *Colletes* (Fig. 3a). This reconstruction implied a very early geodispersal (crown age 27.4 Mya) to the Nearctic from the Neotropics during the late Oligocene. Based on their findings, Kuhlmann et al. (2009) suggested that the Nearctic species groups of earliest divergence—*C. dalaea* and *C. compactus* groups—would be descendants of two different Neotropical ancestors. In other words, the Nearctic would have been colonized at

least twice independently by *Colletes* in their early evolution (Kuhlmann et al., 2009). In our phylogenetic analyses, however, the two groups were recovered as reciprocally monophyletic (Figs. 1 and 2) which supported a single early geodispersal event into the Nearctic. In theory, two possible geodispersal routes could have potentially been used by *Colletes* to the Nearctic: the Isthmus of Panama (IP) and the Antilles. The complete formation of the IP, and the consequent closure of the Central American Seaway (CAS), likely took place 4–3 Mya (Coates and Stallard, 2013). Whereas the crown age of the MRCA of *Colletes* was estimated by us to be *c.* 27 Mya (Fig. 3a), a geodispersal through the IP thus appears improbable. However, more recent studies have unraveled a rather complex geological history according to which the IP may have formed much earlier than currently thought, either in the middle Miocene (Montes et al., 2015) or near the Oligocene-Miocene boundary (Bacon et al., 2015). Even less conservative estimates have depicted the IP as being represented by a chain of islands during the late Eocene (Montes et al., 2012). The MRCA of *Colletes* could alternatively have geodispersed to the Nearctic via the Antilles which, in spite of their gradual movement eastwards since the late Eocene, have maintained a fairly uniform configuration over the past 40 My (Graham, 2018). This scenario, however, is weakened by the fact that the MRCA of all *Colletes* species currently found in the Antilles—*C. granpiedrensis* Genaro, *C. hicaco* Genaro, *C. monteifragus* Raw and *C. submarginatus* (Raw, 1984; Genaro, 2001, 2003; Ascher and Pickering, 2019)—is of fairly recent divergence (crown age 3.7 Mya; see clade 5 in Fig. 3a). There are numerous examples of pre-3.5 Mya geodispersals across the CAS by terrestrial animals documented in the literature (compiled by Bacon et al., 2015), including bees (Hines, 2008; Ramírez et al., 2010; Rasmussen and Cameron, 2010). Although it seems reasonable to consider that the MRCA of *Colletes* could have colonized the Nearctic in the late Oligocene, it nonetheless is highly unlikely that a continuous Pan-American distribution could have been maintained, as suggested by our DEC analysis (Fig. 3a), given the tenuous connection between North and South Americas at that time.

Four late Miocene, back geodispersals into the Neotropics from the Nearctic were inferred by our biogeographic reconstruction (Fig. 3b). The earliest geodispersal events were found at the MRCA of *C. intermixtus* plus *C. latitarsis* (crown age 10.7 Mya), and at that of the *C. nudus* group (crown age 10.3 Mya); whereas the most recent ones were found at the MRCA of *C. bombiformis* plus *C. gilensis* Cockerell (crown age 6.6 Mya), and at that of the *C. compactus* group (crown age 6.2 Mya). This time span coincided with the formation and

expansion of savannah-like and grassland biomes in the Nearctic west, which gradually replaced mixed mesophytic forest that had dominated most of the landscape from 35–10 Mya (Pound et al., 2012; Meseguer et al., 2015). This change in vegetation was likely boosted by the drastic transition from the warm Middle Miocene Climatic Optimum to the glaciation event which lasted from 15–13 Mya (Zachos et al., 2008). By the beginning of the late Miocene, the open-vegetation biomes extended from the North American Great Plains to what is now Southwestern Mexico (Pound et al., 2012; Meseguer et al., 2015) and possibly constituted the geodispersal route used by these four lineages of *Colletes* to reach the Neotropics. The same route may have been taken by the MRCA of *C. latitarsis* and *C. submarginatus* (crown age 4.7 Mya) in the opposite direction. Intriguingly, no lineage interchange between the two realms was inferred for the time period corresponding to the Great American Biotic Interchange (*i.e.* after 3 Mya; Marshall, 1979, 1982; Web, 2006; Woodburne, 2010), although this lies within the 95% HDP for the last two geodispersals.

The Andes uplift has drastically changed the precipitation regime (Rech et al., 2006, 2010), atmospheric CO<sub>2</sub> content (Graham, 2009) and western fluvial system (Hoorn et al., 1995) in South America, ultimately driving continental landscape evolution over the last *c.* 65 My (Hoorn et al., 2010; Coudurier-Curveur et al., 2015). As the longest and second highest cordillera on the planet (Graham, 2009), it is not a surprise that the Andes has contributed to diversification of both plant (*e.g.* Antonelli et al., 2009; Struwe et al., 2009; Strelin et al., 2017) and animal (*e.g.* Brumfield and Edwards, 2007; Weir and Price, 2011; Blandin and Purser, 2013; Almeida et al., 2019) taxa through vicariance. Our ancestral-range reconstruction detected three cladogenetic events within *Colletes* that could potentially be linked to the Andean orogeny, namely, at the MRCAs of *C. arthuri* Ferrari plus *C. ferenudus* Ferrari (crown age 12.6 Mya), *C. rufipes* Smith plus *C. atacamensis* Janvier (crown age 9.2 Mya), and *C. cyaneus* plus *C. cyaniventris* Spinola (crown age 6.8 Mya). Even though the Andes may have begun rising as early as 100 Mya (Cobbold et al., 2007; Armijo et al., 2015), its most pronounced uplift period did not occur until *c.* 12–11 Mya (Hoorn, 2010; Jordan et al., 2014), which could potentially explain why the trans-Andean sister groups are relatively more recent.

Based on our biogeographic reconstruction, *Colletes* would have first geodispersed to the Palaearctic from the Nearctic near the Oligocene-Miocene boundary (OMB, *c.* 23 Mya). This event was inferred for the MRCA of all *Colletes* except clade 1 (crown age 23.4 Mya), which



suggested a very early geodispersal to the OW soon after colonization of the Northern Hemisphere (crown age 27.6 Mya). The Bering Land Bridge (BLB) which had been connecting Alaska and Siberia, at least intermittently, since the late Cretaceous (Sanmartín et al., 2001) was likely the route used by *Colletes*. It should be noted, however, that the OMB was marked by a major glaciation event which succeeded a relatively warm period (c. 27–25 Mya) in the late Oligocene (Mudelsee et al., 2014). Given its close association with the Arctic Circle, climatic conditions in the BLB during the OMB might have been unlikely to permit geodispersal of terrestrial organisms (Sanmartín et al., 2001; Zachos et al., 2001, 2008), particularly ectotherms such as bees. Nevertheless, the BLB has been acknowledged to have served as an important refugium for boreal species during the various Pleistocene glaciations (DeChaine, 2008) and so perhaps it acted similarly during earlier cold periods. Two alternative, trans-Atlantic geodispersal routes may also have been available at that time: the Thulean Bridge which connected the Queen Elizabeth Islands to southern Europe, and the De Geer Bridge which united the Canadian Arctic Archipelago and the Fennoscandian peninsula, both through Greenland (Brikiatis, 2014 and references therein). The former had a warmer climate due to its southern position in relation to the latter (~45°N and >70°N, respectively) and, consequently, has been widely acknowledged as a more likely geodispersal route for terrestrial organisms (e.g. Sanmartín et al., 2001; Irving, 2005; Praz and Packer, 2014). The Thulean and the De Geer Bridges are thought to have existed until the early (c. 50 Mya) and late (c. 40 Mya) Eocene, respectively (Sanmartín et al., 2001; Condamine et al., 2013), both too early for *Colletes* geodispersal. However, it is possible that they may have persisted as island chains up until the early Miocene (Baskin and Baskin, 2016), which could have then allowed stepping-stone geodispersal of cold-adapted *Colletes*. Nevertheless, we do not believe that the ancestor in question had a Holarctic distribution, as inferred by our biogeographic reconstruction (Fig. 3a), given the highly unfavourable climatic conditions in the BLB and the discontinuous nature of the trans-Atlantic connection between the Nearctic and Palaearctic during the OMB.

Lineage exchanges between the NW and OW completely ceased from c. 23–12 Mya, but since then *Colletes* geodispersal between the two at least twice in each direction (Fig. 3a). The earliest geodispersal among the four was found at the MRCA of the Eurasian *C. cunicularius* plus its NW closest relatives, which would have geodispersal from the Nearctic to the Palaearctic near the middle-late Miocene boundary (crown age 11.4 Mya). This finding

corroborated the first biogeographic scenario regarding the origin of *C. cunicularius* hypothesized by Kuhlmann et al. (2009) which implied a single geodispersal event of the ancestor of *C. cunicularius* from the Nearctic to the Palaearctic. Later, two Palaearctic ancestors would have invaded the Nearctic virtually at the same period in the late Miocene: the MRCA of *C. formosus* plus *C. inaequalis* (crown age 10.1 Mya), and that of *C. impunctatus* plus *C. sierrensis* Frey-Gessner (crown age 10.0 Mya). At that time, the only available geodispersal route connecting the two realms would have been the BLB (Sanmartín et al., 2001; Brikiatis, 2014; Graham, 2018). Along with the high latitude regions across the Holarctic, the BLB would have been almost entirely covered with boreal forest which had been replacing mixed mesophytic forest since the early Miocene (Pound et al., 2012; Meseguer et al., 2015; Graham, 2018). The latest geodispersal event was inferred for the MRCA of *C. phaceliae* Cockerell plus *C. sierrensis* which may have geodispersed from the Nearctic to the Palaearctic across the BLB in the Pliocene-Pleistocene boundary (crown age 1.9 Mya). Although the BLB had been submerged since the establishment of the Bering Strait (c. 2.6 Mya), it has been repeatedly exposed as a result of the glaciation events from the late Pliocene through middle Pleistocene (Ehlers and Gibbard, 2007).

Our biogeographic reconstruction indicated that the Afrotropical species of *Colletes* are descendants of at least two Palaearctic ancestors that geodispersed to the Afrotropics in the Miocene (Fig. 3a). The earliest arrival was inferred for the MRCA of *C. escalerae* Noskiewicz/*C. nanus* plus *C. antecessus* Cockerell/*C. aureocinctus* Cockerell which would have invaded the Afrotropics in the middle Miocene (crown age 12.6 Mya). According to our analysis, this ancestor would have later given rise to the bulk of the species that inhabit the realm at present (Fig. 3a). Most of these are endemic to the South African Greater Cape Floristic Region which has been detected as the globally most important centre of species richness of *Colletes* in relative terms (Bystriakova et al., 2018). The most recent arrival in the Afrotropics was found at the MRCA of *C. somereni* plus *C. merceti* Noskiewicz/*C. omanus* which likely arrived in the realm in the latest Miocene (crown age 5.5 Mya). It is possible that both geodispersal events would have occurred via a long, arid corridor constituted by central Asia, the Arabian Peninsula and northern Africa which had been mostly covered with grasslands and savannahs since the Miocene (Senut et al., 2009; Meseguer et al., 2015). These biomes came to replace mixed

mesophytic forest (Asia) and tropical forest (Africa) with the increase of aridification initiated earlier in the Miocene (Meseguer et al., 2015), and likely facilitated geodispersal southwards.

Unfortunately, no ancestral range including the Indo-Malay was inferred in our biogeographic analysis, which prevented us from determining when *Colletes* would have first colonized this realm (Fig. 3a). This was likely a result of us having been able to sample only two Indo-Malayan species—*C. esakii* Hirashima and *C. lacunatus* (Kuhlmann, 1998, 2010; Kuhlmann et al., 2009; Ascher and Pickering, 2019). In fact, both appear to be primarily Palaearctic in distribution, having invaded the Indo-Malay only more recently. This hypothesis is supported by two facts: first, most of their geographic ranges lie within the Palaearctic, and their known occurrence records within the Indo-Malay are close to the border between the two realms (Ascher and Pickering, 2019; M. Kuhlmann, *pers. comm.*). Second, the ancestral ranges of the MRCAs which *C. esakii* and *C. lacunatus* share with their respective sister species were inferred to include only the Palaearctic (Fig. 3a). It is nonetheless certain that the Indo-Malayan realm has been invaded, at least, five times independently by Palaearctic ancestral *Colletes* given that representatives of five species groups of unequivocal Palaearctic origin—*C. caspicus*, *C. clypearis*, *C. lacunatus*, *C. marginatus* and *C. succinctus* groups—are known to occur there (Kuhlmann, 1998, 2010; Kuhlmann et al., 2009; Ascher and Pickering, 2019).

## Conclusion

In accordance with previous studies, our phylogenetic analyses provide further support for the monophyly of *Colletes* and for its sister-group relationship to *Hemicotelles*. The approach of using DNA barcodes to augment our taxon sampling allowed us to consolidate the basis for future classification attempts regarding the *Colletes* of the World. Yet, more data (especially from slowly-evolving loci) are needed to verify whether the poorly-supported groupings recognized herein are truly monophyletic. More specifically, it will be important to confirm (i) whether the *C. acutus* group belongs in none of the currently available subgenera, (ii) whether the members of the *C. similis* group are more closely related to *C. nasutus* rather than to the other groups traditionally considered in *Simcolletes*, and (iii) whether *C. graeffei* is sister to the *C. succinctus* group. Of particular relevance was the fact that we placed the large majority of the Neotropical *Colletes* into a monophyletic suite of species groups for the first time. Nevertheless,

the position of a series of species from the NW within the phylogenetic tree of *Colletes* remains unresolved and therefore further work is needed.

Our attempts to reconstruct the historical biogeography of *Colletes* at a global scale revealed with high confidence that the genus originated somewhere within the Neotropics, most likely within South America, at about 33 Mya. The biogeographic scenario depicted herein includes an early geodispersal to the Nearctic (*c.* 27 Mya) followed by an early arrival in the Palaearctic (*c.* 24 Mya). From there, *Colletes* colonized both the Afrotropic and Indo-Malay realms; the former was likely invaded for the first time at about 12.5 Mya, but unfortunately we could not date the latter event. Future studies should then aim to elucidate which of the South American dominions (*sensu* Morrone, 2014) corresponds to the point of origin of *Colletes*, and when the genus first colonized the Indo-Malay.

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## Appendix I: Supplementary tables

**Table S1.** List of the species sampled and GenBank accession numbers (or voucher codes if sequenced by us) for the sequences used in our analyses. For COI sequences not yet deposited in GenBank, BOLD sample IDs are provided. 28S: 28S rRNA large subunit; COI: cytochrome c oxidase subunit 1; EF1a: elongation factor-1 $\alpha$  copy F2; opsin: long-wavelength rhodopsin; pol II: RNA polymerase II.

Species <sup>1</sup>	Classification <sup>2</sup>	28S	COI	EF1a	opsin	pol II	wingless
<i>Stenotritus</i> sp.	Stenotritidae	DQ872757	–	DQ141115	DQ115564	–	DQ884714
<i>Callomelitta antipodes</i> (Smith)	Callomelittinae	DQ872767	JN603418	AY585122	DQ115563	AY945105	EF032907
<i>Caupolicana vestita</i> (Smith)	Diphaglossinae	DQ872758	KX821018	AY585124	DQ115543	AY945109	DQ884726
<i>Diphaglossa gayi</i> Spinola	Diphaglossinae	DQ872759	KX820649	AY585125	DQ115545	AY945115	DQ884728
<i>Paracolletes</i> aff. <i>crassipes</i> Smith	Diphaglossinae	DQ768473	–	DQ884584	DQ884491	–	DQ884729
<i>Callohesma calliopsella</i> (Cockerell)	Euryglossinae	DQ872768	DQ872696	AY585126	DQ115550	AY945117	DQ884809
<i>Euryglossina globuliceps</i> (Cockerell)	Euryglossinae	DQ872769	DQ872697	AY585127	DQ115551	AY945118	DQ884810
<i>Xanthesma furcifera</i> (Cockerell)	Euryglossinae	DQ872770	–	AY585140	DQ115552	AY945173	DQ884811
<i>Scrapter algoensis</i> (Friese)	Scapterinae	DQ872771	DQ872698	EF032901	EF032904	–	DQ884812
<i>Scrapter erubescens</i> (Friese)	Scapterinae	DQ872772	DQ872699	AY585135	DQ115558	AY945161	DQ884813
<i>Amphylaeus obscuriceps</i> (Friese)	Hylaeinae	DQ768597	–	DQ884687	DQ884564	–	DQ884857
<i>Hylaeus proximus</i> (Smith)	Hylaeinae	DQ872779	DQ872731	AY585130	DQ115548	AY945128	EF032906
<i>Hyleoides concinna</i> (Fabricius)	Hylaeinae	DQ768601	DQ872734	DQ884691	DQ884560	–	DQ884861
<i>Meroglossa itamuca</i> (Cockerell)	Hylaeinae	DQ768604	–	DQ884694	DQ884565	–	DQ884863
<i>Anthoglossa robusta</i> (Cockerell)	Neopasiphaeinae	DQ768475	–	DQ884586	DQ884493	–	DQ884731
<i>Hexanthes missionica</i> Ogloblin	Neopasiphaeinae	DQ768504	–	DQ884615	DQ884520	–	DQ884763
<i>Eulonchopria simplicicrus</i> (Michener)	Neopasiphaeinae	DQ768477	–	DQ884588	DQ884495	–	DQ884734
<i>Leioproctus irroratus</i> (Smith)	Neopasiphaeinae	DQ872765	–	AY585132	DQ115555	AY945131	DQ884788
<i>Perditomorpha leucostoma</i> (Cockerell)	Neopasiphaeinae	DQ768496	–	DQ884607	DQ884513	–	DQ884755
<i>Chilicola longiceps</i> (Ashmead)	Xeromelissinae	RF114	CCDB-28313-F02	RF114	–	–	RF114
<i>Chilicola rostrata</i> (Friese)	Xeromelissinae	DQ768570	DQ872727	DQ884662	DQ884558	–	DQ884829
<i>Geodiscelis longiceps</i> Packer	Xeromelissinae	DQ768544	DQ872700	DQ884655	DQ884551	–	DQ884817
<i>Xenochilicola mamigna</i> Toro & Moldenke	Xeromelissinae	DQ768558	DQ872715	DQ884660	DQ884556	–	DQ884827
<i>Colletes acutus</i> Pérez	Colletinae	EF028578	EF028491	–	–	–	–

<i>Colletes albomaculatus</i> (Lucas)	Colletinae	EF028579	EF028492	–	–	–	–
<i>Colletes alocochila</i> Moure	Colletinae	RF043	CCDB-30345-G12	RF043	RF043	RF043	RF043
<i>Colletes annejohnae</i> Kuhlmann	Colletinae	EF028580	EF028493	–	–	–	–
<i>Colletes antecessus</i> Cockerell	Colletinae	–	EF028529	–	–	–	–
<i>Colletes argentinus</i> Friese	Colletinae	RF047	CCDB-24582-H01	RF047	RF047	RF047	RF047
<i>Colletes arthuri</i> Ferrari	Colletinae	–	CCDB-30345-D07	–	–	–	–
<i>Colletes atacamensis</i> Janvier	Colletinae	RF038	CCDB-30345-H02	RF038	RF038	RF038	RF038
<i>Colletes atripes</i> Smith	Colletinae	RF040	CCDB-30345-G10	RF040	RF040	RF040	RF040
<i>Colletes aureocinctus</i> Cockerell	Colletinae	EF028615	EF028530	–	–	–	–
<i>Colletes aztecus</i> Cresson	Colletinae	–	CCDB-22009-C03	–	–	–	–
<i>Colletes bicolor</i> Smith	Colletinae	DQ768539	DQ872692	DQ884650	DQ884549	–	DQ884802
<i>Colletes bombiformis</i> Metz	Colletinae	–	CCDB-22009-A06	–	–	–	–
<i>Colletes bryanti</i> Timberlake	Colletinae	LP038	CCDB-28238-E03	LP038	LP038	LP038	LP038
<i>Colletes californicus</i> Provancher	Colletinae	LP024	CCDB-24580-C09	LP024	–	LP024	LP024
<i>Colletes capensis</i> Cameron	Colletinae	EF028616	EF218723	–	–	–	–
<i>Colletes cardiurus</i> Cockerell	Colletinae	EF028617	EF028531	–	–	–	–
<i>Colletes claripes</i> Friese	Colletinae	EF028618	EF028532	–	–	–	–
<i>Colletes clypeonitens</i> Swenk	Colletinae	LP027	–	LP027	LP027	LP027	LP027
<i>Colletes cognatus</i> Spinola	Colletinae	RF079	CCDB-30384-C10	RF079	RF079	RF079	RF079
<i>Colletes compactus</i> Cresson	Colletinae	RF105	CCDB-30346-F02	RF105	RF105	RF105	RF105
<i>Colletes conradti</i> Noskiewicz	Colletinae	–	EF028496	–	–	–	–
<i>Colletes cunicularius</i> (Linnaeus)	Colletinae	EF028585	EF028498	–	–	–	–
<i>Colletes cyanescens</i> (Haliday)	Colletinae	RF063	CCDB-30346-D06	RF063	RF063	RF063	RF063
<i>Colletes cyaneus</i> Holmberg	Colletinae	–	CCDB-30344-D09	–	–	–	–
<i>Colletes cyaniventris</i> Spinola	Colletinae	RF073	CCDB-30384-B09	RF073	RF073	RF073	–
<i>Colletes daviesanus</i> Smith	Colletinae	RF025	CCDB-28312-H11	RF025	RF025	RF025	RF025
<i>Colletes distinctus</i> Cresson	Colletinae	DQ768530	DQ872683	–	–	–	–
<i>Colletes eardleyi</i> Kuhlmann	Colletinae	EF028631	EF028545	–	–	–	–
<i>Colletes eous</i> Morice	Colletinae	EF028588	EF028501	–	–	–	–
<i>Colletes esakii</i> Hirashima	Colletinae	EF028589	EF028502	–	–	–	–
<i>Colletes escaleraei</i> Noskiewicz	Colletinae	EF028590	EF028503	–	–	–	–
<i>Colletes eulophi</i> Robertson	Colletinae	LP028	CCDB-30344-B07	LP028	LP028	LP028	LP028



<i>Colletes ferenudus</i> Ferrari	Colletinae	—	CCDB-24581-A09	—	—	—	—
<i>Colletes flaminii</i> Moure	Colletinae	RF072	CCDB-30384-B07	RF072	RF072	RF072	RF072
<i>Colletes flavipilosus</i> Ferrari	Colletinae	RF108	CCDB-30384-H04	RF108	RF108	—	RF108
<i>Colletes fodiens</i> (Fourcroy)	Colletinae	RF052	CCDB-28312-A10	RF052	RF052	RF052	RF052
<i>Colletes formosus</i> Pérez	Colletinae	EF028592	EF028505	—	—	—	—
<i>Colletes fulvipes</i> Spinola	Colletinae	RF077	CCDB-30384-C06	RF077	RF077	—	RF077
<i>Colletes furfuraceus</i> Holmberg	Colletinae	DQ768540	DQ872693	DQ884651	DQ884550	—	DQ884803
<i>Colletes fusconotus</i> Cockerell	Colletinae	EF028619	EF028533	—	—	—	—
<i>Colletes gallicus</i> Rodoszkowski	Colletinae	EF028619	EF028619	—	—	—	—
<i>Colletes gilensis</i> Cockerell	Colletinae	LP040	CCDB-28238-C01	LP040	LP040	LP040	LP040
<i>Colletes</i> aff. <i>gilensis</i>	Colletinae	LP041	CCDB-28238-E01	LP041	LP041	LP041	LP041
<i>Colletes gilvus</i> Vachal	Colletinae	RF017	CCDB-15274-A04	RF017	RF017	RF017	RF017
<i>Colletes graeffei</i> Alfken	Colletinae	RF111	CCDB-30345-E12	RF111	RF111	RF111	RF111
<i>Colletes hederæ</i> Schmidt & Westrich	Colletinae	EF028598	EF028511	—	—	—	—
<i>Colletes hylaeiformis</i> Eversmann	Colletinae	RF095	CCDB-30385-F05	RF095	RF095	RF095	RF095
<i>Colletes impunctatus</i> Nylander	Colletinae	EF028600	EF028512	—	—	—	—
<i>Colletes inaequalis</i> Say	Colletinae	RF115	CCDB-30386-G02	RF115	RF115	RF115	RF115
<i>Colletes intermixtus</i> Swenk	Colletinae	LP044	CCDB-28238-C07	—	LP044	LP044	LP044
<i>Colletes kincaidii</i> Cockerell	Colletinae	LP030	CCDB-24580-B04	LP030	LP030	LP030	LP030
<i>Colletes kuhlmanni</i> Ferrari	Colletinae	RF015	CCDB-30345-D01	RF015	RF015	RF015	RF015
<i>Colletes lacunatus</i> Dours	Colletinae	EF028603	EF028515	—	—	—	—
<i>Colletes larreae</i> Timberlake	Colletinae	LP045	CCDB-24580-B06	LP045	LP045	—	LP045
<i>Colletes latitarsis</i> Robertson	Colletinae	RF026	CCDB-28312-H09	RF026	RF026	RF026	RF026
<i>Colletes louisae</i> Cockerell	Colletinae	LP046	CCDB-28238-C09	LP046	LP046	LP046	LP046
<i>Colletes lucens</i> Vachal	Colletinae	RF042	CCDB-30345-H06	RF042	RF042	RF042	RF042
<i>Colletes mandibularis</i> Smith	Colletinae	—	CCDB-28238-C11	LP048	LP048	LP048	LP048
<i>Colletes marleyi</i> Cockerell	Colletinae	EF028623	EF028537	—	—	—	—
<i>Colletes merceti</i> Noskiewicz	Colletinae	RF082	CCDB-30345-F07	—	—	—	RF082
<i>Colletes meridionalis</i> Schrottky	Colletinae	RF020	CCDB-30345-D11	RF020	RF020	RF020	RF020
<i>Colletes mimincus</i> Cockerell	Colletinae	RF023	CCDB-24581-F03	RF023	RF023	RF023	RF023
<i>Colletes murinus</i> Friese	Colletinae	RF071	—	RF071	RF071	RF071	RF071
<i>Colletes musculus</i> Friese	Colletinae	RF046	CCDB-30345-H09	RF046	RF046	RF046	RF046

<i>Colletes nanus</i> Friese	Colletinae	EF028605	EF028518	–	–	–	–
<i>Colletes nasutus</i> Smith	Colletinae	–	HM401158	–	–	–	–
<i>Colletes nigrutilus</i> Friese	Colletinae	RF016	CCDB-30345-D03	RF016	RF016	RF016	RF016
<i>Colletes nigropilosus</i> Ferrari	Colletinae	RF045	–	–	–	–	RF045
<i>Colletes nudus</i> Robertson	Colletinae	RF054	CCDB-30345-C02	RF054	RF054	RF054	RF054
<i>Colletes omanus</i> Kuhlmann	Colletinae	EF028607	EF028520	–	–	–	–
<i>Colletes opacus</i> Friese	Colletinae	EF028624	EF028538	–	–	–	–
<i>Colletes patagonicus</i> Schrottky	Colletinae	RF078	CCDB-30384-C08	RF078	RF078	–	RF078
<i>Colletes perezi</i> Morice	Colletinae	RF112	CCDB-30345-F12	–	RF112	RF112	RF112
<i>Colletes perileucus</i> Cockerell	Colletinae	LP050	CCDB-24580-D10	–	LP050	LP050	LP050
<i>Colletes peruvicus</i> Cockerell	Colletinae	RF022	CCDB-24581-E12	RF022	RF022	RF022	RF022
<i>Colletes petropolitanus</i> Dalla Torre	Colletinae	RF019	CCDB-30345-D09	RF019	RF019	RF019	RF019
<i>Colletes phacelliae</i> Cockerell	Colletinae	LP051	–	LP051	LP051	LP051	LP051
<i>Colletes quelu</i> Rojas & Toro	Colletinae	RF039	CCDB-30345-H01	–	–	–	–
<i>Colletes roborovskyi</i> Friese	Colletinae	EF028609	EF028522	–	–	–	–
<i>Colletes rufipes</i> Smith	Colletinae	RF050	CCDB-24582-H03	RF050	RF050	RF050	RF050
<i>Colletes rugicollis</i> Friese	Colletinae	RF062	CCDB-30346-D04	RF062	RF062	RF062	RF062
<i>Colletes scopiventer</i> Swenk	Colletinae	LP032	CCDB-24580-C01	LP032	LP032	LP032	LP032
<i>Colletes sierrensis</i> Frey-Gessner	Colletinae	EF028610	EF028523	–	–	–	–
<i>Colletes similis</i> Schenck	Colletinae	RF051	CCDB-28312-H10	RF051	RF051	RF051	RF051
<i>Colletes simulans</i> Cresson	Colletinae	RF055	CCDB-30345-G06	RF055	–	RF055	RF055
<i>Colletes solidaginis</i> Swenk	Colletinae	LP053	CCDB-30345-C10	LP053	LP053	LP053	LP053
<i>Colletes somereni</i> Cockerell	Colletinae	RF024	CCDB-30384-B03	RF024	RF024	RF024	RF024
<i>Colletes sororcula</i> Cockerell	Colletinae	–	EF028539	–	–	–	–
<i>Colletes speculiferus</i> Cockerell <sup>3</sup>	Colletinae	RF069	CCDB-30346-E03	RF069	RF069	RF069	RF069
<i>Colletes striginasis</i> Vachal	Colletinae	RF021	CCDB-24581-G02	RF021	RF021	RF021	RF021
<i>Colletes submarginatus</i> Cresson	Colletinae	–	109-CU <sup>4</sup>	–	–	–	–
<i>Colletes succinctus</i> (Linnaeus)	Colletinae	EF028612	EF028525	–	–	–	–
<i>Colletes susannae</i> Swenk	Colletinae	RF053	CCDB-30345-B11	RF053	RF053	RF053	RF053
<i>Colletes</i> aff. <i>susannae</i>	Colletinae	LP055	CCDB-24580-D12	LP055	LP055	LP055	LP055
<i>Colletes tectiventris</i> Timberlake	Colletinae	LP034	CCDB-28238-A09	LP034	LP034	LP034	LP034
<i>Colletes thysanellae</i> Mitchell	Colletinae	RF032	CCDB-24582-H09	RF032	RF032	RF032	RF032

<i>Colletes timberlakei</i> Stephen	Colletinae	LP025	CCDB-28238-A03	LP025	—	LP025	LP025
<i>Colletes willistoni</i> Robertson	Colletinae	RF033	CCDB-24580-A01	RF033	—	RF033	RF033
<i>Colletes wolffi</i> Kuhlmann	Colletinae	EF028614	EF028527	—	—	—	—
<i>Colletes wootoni</i> Cockerell	Colletinae	LP035	CCDB-30344-B03	LP035	LP035	LP035	LP035
<i>Colletes</i> sp. 1	Colletinae	—	ARG-09809-46	—	—	—	—
<i>Colletes</i> sp. 2 <sup>5</sup>	Colletinae	EF028565	EF028482	—	—	—	—
<i>Colletes</i> sp. 3	Colletinae	—	BB2990 <sup>6</sup>	—	—	—	—
<i>Colletes</i> sp. 4	Colletinae	—	BB2811 <sup>6</sup>	—	—	—	—
<i>Colletes</i> sp. 5	Colletinae	—	B03772-A07	—	—	—	—
<i>Colletes</i> sp. 6	Colletinae	—	B03772-A05	—	—	—	—
<i>Colletes</i> sp. 7	Colletinae	—	B03772-A02	—	—	—	—
<i>Colletes</i> sp. 8	Colletinae	—	CCDB-09669-G05	—	—	—	—
<i>Colletes</i> sp. 9	Colletinae	—	CCDB-09842-B05	—	—	—	—
<i>Colletes</i> sp. 10	Colletinae	—	CCDB-09841-B07	—	—	—	—
<i>Colletes</i> sp. 11	Colletinae	—	CCDB-24581-H07	—	—	—	—
<i>Hemicotelles ruizii</i> (Herbst)	Colletinae	RF030	CCDB-24581-F09	RF030	RF030	RF030	RF030
<i>Mourecotelles mixtus</i> Toro & Cabezas	Colletinae	RF056	CCDB-30346-C03	RF056	RF056	RF056	RF056
<i>Mourecotelles moldenkei</i> Toro & Cabezas	Colletinae	RF080	CCDB-30384-C12	RF080	RF080	RF080	RF080
<i>Xanthocotelles adesmiae</i> Toro & Cabezas	Colletinae	RF029	CCDB-30385-D01	RF029	RF029	RF029	RF029
<i>Xanthocotelles aisen</i> Toro & Cabezas	Colletinae	RF076	CCDB-30384-C04	RF076	RF076	RF076	RF076
<i>Xanthocotelles atacama</i> Toro & Cabezas	Colletinae	RF061	CCDB-30346-D02	RF061	RF061	RF061	RF061
<i>Xanthocotelles fritzi</i> Toro & Cabezas	Colletinae	RF060	CCDB-30346-C11	RF060	RF060	RF060	RF060
<i>Xanthocotelles sicheli</i> (Vachal)	Colletinae	RF107	CCDB-30384-H10	RF107	RF107	RF107	RF107

<sup>1</sup>The generic classification of Colletinae adopted herein follows Toro and Cabezas (1977, 1978).

<sup>2</sup>Subfamilies of Colletidae recognized by Almeida et al. (2019).

<sup>3</sup>Species originally identified as *C. mitchelli* Stephen which is a junior synonym of *C. speculiferus* according to Hall et al. (2016).

<sup>4</sup>Sequence generously provided to us by Julio Genaro.

<sup>5</sup>This species corresponds to *Colletes* sp. 1(1) of Kuhlmann et al. (2009).

<sup>6</sup>Sequence generously provided to us by Berry Brosi.

**Table S2.** List of the studied specimens with their locality, identification and repository data. Identifiers are abbreviated as follows: MK (Michael Kuhlmann), TO (Thomas Onuferko) and RF (Rafael Ferrari). Literature whereupon identifications were based are abbreviated as follows: B2017 (Balboa et al., 2017), C1868 (Cresson, 1868), C1913 (Cockerell, 1913), C1914 (Cockerell, 1914), F2017 (Ferrari, 2017), F2019 (Ferrari, 2019), G2003 (Genaro, 2003), K2013 (Kuhlmann and Pauly, 2013), K2014 (Kuhlmann and Proshchalykin, 2014), M2017 (Miklasevskaya, 2017), Ortiz-Sánchez et al., (2004), S1954 (Stephen, 1954), T1977 (Toro and Cabezas, 1977), T1978 (Toro and Cabezas, 1978). Repositories are abbreviated as follows: PCYU (Packer Collection at York University, Canada), RPSP (Coleção Entomológica Prof. J. M. F. Camargo, Brazil).

Species <sup>1</sup>	Voucher	Sex	Identifier	Reference	Locality	Repository
<i>Chilicola longiceps</i>	RF114	♂	RF	M2017	St. Vincent and the Granadines, St. George, Majorca Mountains	PCYU
<i>Colletes alocochila</i>	RF043	♀	RF	F2017	Chile, Region II, E of San Pedro de Atacama	PCYU
<i>Colletes argentinus</i>	RF047	♀	RF	F2019	Brazil, Rio Grande do Sul, E of Santana do Livramento	PCYU
<i>Colletes arthuri</i>	RF018	♀	RF	F2017	Chile, Region I, SW of Pucará de Copaquilla	PCYU
<i>Colletes aztecus</i>	LP036	♀	RF	C1868	Mexico, Colima, W of Biosphere Reserve Sierra de Manantlán	PCYU
<i>Colletes atacamensis</i>	RF038	♀	RF	F2017	Chile, Region II, E of San Pedro de Atacama	PCYU
<i>Colletes atripes</i>	RF040	♀	RF	F2017	Chile, Region III, Cuesta Castaño	PCYU
<i>Colletes bombiformis</i>	LP037	♀	RF	B2017	Mexico, Jalisco, Rancho los Cortes	PCYU
<i>Colletes bryanti</i>	LP038	♂	TO	S1954	USA, Arizona, Mount Graham	PCYU
<i>Colletes californicus</i>	LP024	♀	TO	S1954	USA, California, R. J. Bernard Field Station	PCYU
<i>Colletes clypeonitens</i>	LP027	♂	TO	S1954	USA, California, SW of Whitewater	PCYU
<i>Colletes cognatus</i>	RF079	♂	RF	F2017	Chile, Region XI, Río Jeinimeni	PCYU
<i>Colletes compactus</i>	RF105	♂	TO	S1954	USA, Arizona, Onion Saddle	PCYU
<i>Colletes cyanescens</i>	RF063	♀	RF	F2017	Chile, Region Metropolitana, Cuesta Zapata	PCYU
<i>Colletes cyaneus</i>	12.3947	♀	RF	F2019	Brazil, Rio Grande do Sul, Santana do Livramento	RPSP
<i>Colletes cyaniventris</i>	RF073	♂	RF	F2017	Chile, Region VIII, S of Lago G. Carrera	PCYU
<i>Colletes daviesanus</i>	RF025	♂	RF	K2014	Kazakhstan, Akmola, Astana	PCYU
<i>Colletes eulophi</i>	LP028	♂	TO	S1954	USA, Arizona, Santa Catalina Mountains	PCYU
<i>Colletes ferenudus</i>	12.4017	♀	RF	F2019	Brazil, Rio Grande do Sul, NNE of Pedras Altas	RPSP
<i>Colletes flaminii</i>	RF072	♀	RF	F2017	Chile, Region XI, Río Jeinimeni	PCYU
<i>Colletes flavipilosus</i>	RF108	♀	RF	F2017	Chile, Region VII, Laguna del Teno	PCYU
<i>Colletes fodiens</i>	RF052	♀	RF	O2004	Portugal, Setubal, Costa da Caparica	PCYU
<i>Colletes fulvipes</i>	RF077	♂	RF	F2017	Chile, Region XI, Río Jeinimeni	PCYU
<i>Colletes gilensis</i> (1)	LP039	♂	TO	S1954	USA, New Mexico, Gila National Forest	PCYU
<i>Colletes gilensis</i> (2)	LP040	♂	TO	S1954	USA, New Mexico, Gila National Forest	PCYU

<i>Colletes aff. gilensis</i>	LP041	♀	TO	S1954	USA, Arizona, Mount Graham	PCYU
<i>Colletes gilvus</i> (1)	RF017	♂	RF	F2017	Chile, Region I, SW of Pucará de Copaquilla	PCYU
<i>Colletes gilvus</i> (2)	LP042	♂	RF	F2017	Chile, Region XV, N of Zapahuira	PCYU
<i>Colletes graeffei</i>	RF111	♀	MK	expert	Hungary, Central Hungary, Budaors	PCYU
<i>Colletes hylaeiformis</i>	RF095	♂	MK	expert	Hungary, Central Hungary, Torokbalint	PCYU
<i>Colletes inaequalis</i>	RF115	♀	TO	S1954	Canada, Ontario, Toronto	PCYU
<i>Colletes intermixtus</i> (1)	LP043	♂	TO	S1954	USA, Utah, W of Hyrum Dam	PCYU
<i>Colletes intermixtus</i> (2)	LP044	♂	TO	S1954	USA, Utah, W of Hyrum Dam	PCYU
<i>Colletes kincaidii</i> (1)	LP030	♂	TO	S1954	Canada, Ontario, Navan	PCYU
<i>Colletes kincaidii</i> (2)	LP031	♀	TO	S1954	Canada, Ontario, Vaughan	PCYU
<i>Colletes kuhlmanni</i>	RF015	♂	RF	F2017	Chile, Region IV, NE of Aduanas	PCYU
<i>Colletes larreae</i>	LP045	♀	TO	S1954	USA, California, SW of Riverside County	PCYU
<i>Colletes latitarsis</i>	RF026	♀	TO	S1954	Canada, Ontario, Derrydowns Park	PCYU
<i>Colletes louisae</i>	LP046	♀	TO	S1954	USA, California, Lake Isabella	PCYU
<i>Colletes lucens</i>	RF042	♂	RF	F2017	Chile, Region VII, Los Queñes	PCYU
<i>Colletes mandibularis</i> (1)	LP047	♀	TO	S1954	USA, California, E of Onyx	PCYU
<i>Colletes mandibularis</i> (2)	LP048	♀	TO	S1954	USA, California, Onyx	PCYU
<i>Colletes merceti</i>	RF082	♂	MK	expert	Spain, Andaluzia, Almeria	PCYU
<i>Colletes meridionalis</i>	RF020	♂	RF	F2019	Brazil, Minas Gerais, RPPN Cachoeira do Campo	PCYU
<i>Colletes mimincus</i>	RF023	♀	RF	C1914	Peru, Lima, Lunahuaná Valley	PCYU
<i>Colletes murinus</i>	RF071	♀	RF	F2017	Peru, Lima, Lunahuaná Valley	PCYU
<i>Colletes musculus</i>	RF046	♀	RF	F2017	Chile, VII, E of Aduanas	PCYU
<i>Colletes nigrifulus</i>	RF016	♂	RF	F2017	Chile, Region VII, Rio Teno	PCYU
<i>Colletes nigropilosus</i>	RF045	♀	RF	F2017	Chile, Region II, S of Caspana	PCYU
<i>Colletes nudus</i>	RF054	♀	TO	S1954	Canada, Ontario, Rondeau Provincial Park	PCYU
<i>Colletes patagonicus</i>	RF078	♂	RF	F2017	Chile, Region XI, Río Jeinimeni	PCYU
<i>Colletes perezi</i>	RF112	♀	MK	expert	Tunisia, Gabes, Matmata	PCYU
<i>Colletes perileucus</i> (1)	LP049	♀	TO	S1954	USA, Arizona, Pima Canyon Trail	PCYU
<i>Colletes perileucus</i> (2)	LP050	♂	TO	S1954	USA, Arizona, Pima Canyon Trail	PCYU
<i>Colletes peruvicus</i>	RF022	♂	RF	C1913	Peru, Huancavelica, Pisco Valley	PCYU
<i>Colletes petropolitanus</i>	RF019	♀	RF	F2019	Brazil, Minas Gerais, Poços de Caldas	PCYU
<i>Colletes phaceliae</i>	LP051	♂	TO	S1954	USA, Colorado, Denver County	PCYU

<i>Colletes quelu</i>	RF039	♀	RF	F2017	Chile, Region I, SW of Alca	PCYU
<i>Colletes rufipes</i>	RF050	♂	RF	F2019	Brazil, Minas Gerais, São Gonçalo do Rio das Pedras	PCYU
<i>Colletes rugicollis</i>	RF062	♂	RF	F2019	Peru, San Martín, Source of Río Negro	PCYU
<i>Colletes scopiventer</i>	LP032	♀	TO	S1954	USA, Arizona, NE of Douglas	PCYU
<i>Colletes similis</i>	RF051	♂	RF	K2014	Iran, Tehran, Meygun	PCYU
<i>Colletes simulans</i>	RF055	♂	TO	S1954	Canada, Ontario, Sandbanks Provincial Park	PCYU
<i>Colletes solidaginis</i> (1)	LP052	♀	TO	S1954	Canada, Ontario, Rondeau Provincial Park	PCYU
<i>Colletes solidaginis</i> (2)	LP053	♀	TO	S1954	Canada, Ontario, Rondeau Provincial Park	PCYU
<i>Colletes somereni</i>	RF024	♂	RF	K2013	Kenya, Turkana, Turkana Basin Institute	PCYU
<i>Colletes speculiferus</i>	RF031	♂	TO	S1954	USA, North Carolina, Kill Devil Hills	PCYU
<i>Colletes striginasis</i>	RF021	♂	RF	C1913	Peru, Huancavelica, Pisco Valley	PCYU
<i>Colletes submarginatus</i>	RF057	♀	RF	G2003	Cuba, Fosforita, San José de Las Lajas	PCYU
<i>Colletes susannae</i>	RF053	♀	TO	S1954	Canada, Ontario, Rondeau Provincial Park	PCYU
<i>Colletes aff. susannae</i> (1)	LP054	♀	TO	S1954	USA, Texas, Chaparral Wildlife Management Area	PCYU
<i>Colletes aff. susannae</i> (2)	LP055	♂	TO	S1954	USA, Texas, Chaparral Wildlife Management Area	PCYU
<i>Colletes tectiventrís</i>	LP034	♂	TO	S1954	USA, Arizona, W of Willcox	PCYU
<i>Colletes thysanellae</i>	RF032	♀	TO	S1954	USA, North Carolina, Kill Devil Hills	PCYU
<i>Colletes timberlakei</i> (1)	LP025	♀	TO	S1954	USA, Colorado, Bellvue	PCYU
<i>Colletes timberlakei</i> (2)	LP026	♀	TO	S1954	USA, Colorado, Bellvue	PCYU
<i>Colletes willistoni</i>	RF033	♂	TO	S1954	Canada, Ontario, Point Pelee National Park	PCYU
<i>Colletes wootoni</i>	LP035	♂	TO	S1954	USA, New Mexico, S of Animas	PCYU
<i>Colletes</i> sp. 11	LP056	♀	—	—	Nicaragua, San Juan del Sur, El Ostional	PCYU
<i>Hemicotelles ruizii</i>	RF030	♂	RF	T1977	Chile, Region IV, South of Vicuña	PCYU
<i>Mourecotelles mixtus</i>	RF056	♂	RF	T1977	Chile, Region III, W of Domeyko	PCYU
<i>Mourecotelles moldenkei</i>	RF080	♂	RF	T1977	Chile, Region XI, Río Jeinimeni	PCYU
<i>Xanthocotelles adesmiae</i>	RF029	♂	RF	T1978	Chile, Region XI, Río Jeinimeni	PCYU
<i>Xanthocotelles aisen</i>	RF076	♀	RF	T1978	Chile, Region XI, Río Jeinimeni	PCYU
<i>Xanthocotelles atacama</i>	RF061	♂	RF	T1978	Chile, Region IV, Los Lavaderos	PCYU
<i>Xanthocotelles fritzi</i>	RF060	♀	RF	T1978	Chile, Region IV, W of Tilama	PCYU
<i>Xanthocotelles sicheli</i>	RF107	♀	RF	T1978	Chile, Region IX, Cuesta las Raices	PCYU

<sup>1</sup>The generic classification of Colletinae adopted herein follows Toro and Cabezas (1977, 1978).

<sup>2</sup>Species originally identified as *C. mitchelli* Stephen which is a junior synonym of *C. speculiferus* according to Hall et al. (2016).



**Table S3.** List of the species for which DNA barcodes (COI sequences) were obtained from BOLD. Listed here are also the references where the barcodes were originally published and the primers used in the amplifications. For primer sequences consult Table S4. BIN: Barcode Index Number.

Species <sup>1</sup>	Sample ID	BIN	Reference	Primers
<i>Chilicola longiceps</i>	CCDB-28313-F02	BOLD:ADC8820	this study	LepF1/LepR1
<i>Colletes alocochila</i>	CCDB-30345-G12	BOLD:ACW1920	this study	LepF1/LepR1
<i>Colletes argentinus</i>	CCDB-24582-H01	BOLD:AAI9260	Ferrari (2019)	LepF1/LepR1
<i>Colletes arthuri</i>	CCDB-30345-D07	BOLD:AAN4840	this study	LepF1/LepR1
<i>Colletes atacamensis</i>	CCDB-30345-H02	BOLD:AAJ6725	this study	LepF1/LepR1
<i>Colletes atripes</i>	CCDB-30345-G10	BOLD:AAF4094	this study	LepF1/LepR1
<i>Colletes aztecus</i>	CCDB-22009-C03	BOLD:AAI9251	this study	LepF1/LepR1
<i>Colletes bombiformis</i>	CCDB-22009-A06	BOLD:AAI9278	this study	LepF1/LepR1
<i>Colletes bryanti</i>	CCDB-28238-E03	not available	this study	LepF1/LepR1
<i>Colletes californicus</i>	CCDB-24580-C09	BOLD:ABZ4529	Onuferko (2018)	LepF1/LepR1
<i>Colletes cognatus</i>	CCDB-30384-C10	BOLD:ABA0479	this study	C_LepFolF/C_LepFolR
<i>Colletes compactus</i>	CCDB-30346-F02	BOLD:AAC3237	this study	LepF1/LepR1
<i>Colletes cyanescens</i>	CCDB-30346-D06	BOLD:ABY2997	this study	LepF1/LepR1
<i>Colletes cyaneus</i>	CCDB-30344-D09	BOLD:ADI1118	Ferrari (2019)	LepF1/LepR1
<i>Colletes cyaniventris</i>	CCDB-30384-B09	BOLD:AAV8114	this study	C_LepFolF/C_LepFolR
<i>Colletes daviesanus</i>	CCDB-28312-H11	BOLD:AAI9262	this study	LepF1/LepR1
<i>Colletes eulophi</i>	CCDB-30344-B07	BOLD:ABZ4837	this study	LepF1/LepR1
<i>Colletes ferenudus</i>	CCDB-24581-A09	BOLD:ACV1831	Ferrari (2019)	C_LepFolF/C_LepFolR
<i>Colletes flaminii</i>	CCDB-30384-B07	BOLD:AAO3445	this study	C_LepFolF/C_LepFolR
<i>Colletes flavipilosus</i>	CCDB-30384-H04	BOLD:AAO3408	this study	C_LepFolF/C_LepFolR
<i>Colletes fodiens</i>	CCDB-28312-A10	BOLD:ABZ6809	this study	LepF1/LepR1
<i>Colletes fulvipes</i>	CCDB-30384-C06	BOLD:AAO3473	this study	C_LepFolF/C_LepFolR
<i>Colletes gilensis</i>	CCDB-28238-C01	BOLD:AAI9270	this study	LepF1/LepR1
<i>Colletes aff. gilensis</i>	CCDB-28238-E01	BOLD:ACV1508	this study	LepF1/LepR1
<i>Colletes gilvus</i>	CCDB-15274-A04	BOLD:AAJ7575	this study	LepF1/LepR1
<i>Colletes graeffei</i>	CCDB-30345-E12	BOLD:AAR9982	this study	LepF1/LepR1
<i>Colletes hylaeiformis</i>	CCDB-30385-F05	BOLD:AAJ7533	this study	RonMWASPdeg_t1/LepR1

<i>Colletes inaequalis</i>	CCDB-30386-G02	BOLD:AAE1758	this study	LepF1/LepR1
<i>Colletes intermixtus</i>	CCDB-28238-C07	BOLD:ACZ7927	Onuferko (2018)	LepF1/LepR1
<i>Colletes kincaidii</i>	CCDB-24580-B04	BOLD:AAB6621	Onuferko (2018)	LepF1/LepR1
<i>Colletes kuhlmanni</i>	CCDB-30345-D01	BOLD:AAO3265	this study	LepF1/LepR1
<i>Colletes larreae</i>	CCDB-24580-B06	BOLD:AAF4108	this study	LepF1/LepR1
<i>Colletes latitarsis</i>	CCDB-28312-H09	BOLD:AAI9271	Onuferko (2018)	LepF1/LepR1
<i>Colletes louisae</i>	CCDB-28238-C09	BOLD:ACF2683	this study	LepF1/LepR1
<i>Colletes lucens</i>	CCDB-30345-H06	BOLD:ACC8448	this study	LepF1/LepR1
<i>Colletes mandibularis</i>	CCDB-28238-C11	BOLD:AAP9596	this study	LepF1/LepR1
<i>Colletes merceti</i>	CCDB-30345-F07	BOLD:ADJ3638	this study	LepF1/LepR1
<i>Colletes meridionalis</i>	CCDB-30345-D11	BOLD:ADF9673	Ferrari (2019)	LepF1/LepR1
<i>Colletes mimincus</i>	CCDB-24581-F03	BOLD:ADJ0654	this study	C_LepFolF/C_LepFolR
<i>Colletes musculus</i>	CCDB-30345-H09	BOLD:ACW1675	this study	LepF1/LepR1
<i>Colletes nigrutilus</i>	CCDB-30345-D03	BOLD:AAV9330	this study	RonMWASPdeg_t1/LepR1
<i>Colletes nigropilosus</i>	CCDB-30345-G09	BOLD:ACW1706	this study	LepF1/LepR1
<i>Colletes nudus</i>	CCDB-30345-C02	BOLD:AAR9947	this study	LepF1/LepR1
<i>Colletes patagonicus</i>	CCDB-30384-C08	BOLD:AAO3408	this study	C_LepFolF/C_LepFolR
<i>Colletes perezi</i>	CCDB-30345-F12	BOLD:AAV9329	this study	LepF1/LepR1
<i>Colletes perileucus</i>	CCDB-24580-D10	BOLD:AAF0982	this study	LepF1/LepR1
<i>Colletes peruvicus</i>	CCDB-24581-E12	BOLD:ADJ4288	this study	C_LepFolF/C_LepFolR
<i>Colletes petropolitanus</i>	CCDB-30345-D09	BOLD:AAR9968	Ferrari (2019)	LepF1/LepR1
<i>Colletes quehu</i>	CCDB-30345-H01	BOLD:ACK8809	this study	LepF1/LepR1
<i>Colletes rufipes</i>	CCDB-24582-H03	BOLD:ADG1971	Ferrari (2019)	LepF1/LepR1
<i>Colletes rugicollis</i>	CCDB-30346-D04	BOLD:ADL4590	this study	LepF1/LepR1
<i>Colletes scopiventer</i>	CCDB-24580-C01	BOLD:AAJ7578	Onuferko (2018)	LepF1/LepR1
<i>Colletes similis</i>	CCDB-28312-H10	BOLD:AAD4051	this study	LepF1/LepR1
<i>Colletes simulans</i>	CCDB-30345-G06	BOLD:AAC0970	Onuferko (2018)	LepF1/LepR1
<i>Colletes solidaginis</i>	CCDB-30345-C10	BOLD:AAI9261	this study	LepF1/LepR1
<i>Colletes somereni</i>	CCDB-30384-B03	BOLD:ADM8400	this study	C_LepFolF/C_LepFolR
<i>Colletes speculiferus</i> <sup>2</sup>	CCDB-30346-E03	BOLD:ACF5111	this study	LepF1/LepR1
<i>Colletes striginasis</i>	CCDB-24581-G02	BOLD:ADJ1960	this study	C_LepFolF/C_LepFolR
<i>Colletes submarginatus</i>	109-CU	BOLD:AAR9951	this study <sup>3</sup>	LCO1490/HCO2198

<i>Colletes susannae</i>	CCDB-30345-B11	BOLD:ADI5579	this study	LepF1/LepR1
<i>Colletes</i> aff. <i>susannae</i>	CCDB-24580-D12	BOLD:ADI5378	this study	LepF1/LepR1
<i>Colletes tectiventris</i>	CCDB-28238-A09	BOLD:ACX1219	Onuferko (2018)	LepF1/LepR1
<i>Colletes thysanellae</i>	CCDB-24582-H09	BOLD:ADF9189	this study	LepF1/LepR1
<i>Colletes timberlakei</i>	CCDB-28238-A03	BOLD:ACZ9863	Onuferko (2018)	LepF1/LepR1
<i>Colletes willistoni</i>	CCDB-24580-A01	BOLD:ACC7841	Onuferko (2018)	LepF1/LepR1
<i>Colletes wootoni</i>	CCDB-30344-B03	BOLD:AAI9255	Onuferko (2018)	LepF1/LepR1
<i>Colletes</i> sp. 1	ARG-09809-46	BOLD:AAZ3615	this study	LepF1/LepR1
<i>Colletes</i> sp. 3	BB2990	BOLD:AAU4177	this study <sup>4</sup>	LepF1/LepR1
<i>Colletes</i> sp. 4	BB2811	BOLD:ABA2823	this study <sup>4</sup>	RonMWASPdeg_t1/LepR1
<i>Colletes</i> sp. 5	B03772-A07	BOLD:ABY6834	this study	LepF1/LepR1
<i>Colletes</i> sp. 6	B03772-A05	BOLD:AAG7494	this study	LepF1/LepR1
<i>Colletes</i> sp. 7	B03772-A02	BOLD:AAI9245	this study	LepF1/LepR1
<i>Colletes</i> sp. 8	CCDB-09669-G05	BOLD:AAZ2365	this study	LepF1/LepR1
<i>Colletes</i> sp. 9	CCDB-09842-B05	BOLD:AAI9274	this study	LepF1/LepR1
<i>Colletes</i> sp. 10	CCDB-09841-B07	BOLD:AAJ7525	this study	LepF1/LepR1
<i>Colletes</i> sp. 11	CCDB-24581-H07	BOLD:ADI5421	this study	C_LepFolF/C_LepFolR
<i>Hemicotelles ruizii</i>	CCDB-24581-F09	BOLD:AAX1332	this study	C_LepFolF/C_LepFolR
<i>Mourecotelles mixtus</i>	CCDB-30346-C03	BOLD:AAK6562	this study	LepF1/LepR1
<i>Mourecotelles moldenkei</i>	CCDB-30384-C12	BOLD:ADM9205	this study	C_LepFolF/C_LepFolR
<i>Xanthocotelles adesmiae</i>	CCDB-30385-D01	BOLD:AAO3410	this study	RonMWASPdeg_t1/LepR1
<i>Xanthocotelles aisen</i>	CCDB-30384-C04	BOLD:ADM7232	this study	LepF1/LepR1
<i>Xanthocotelles atacama</i>	CCDB-30346-D02	BOLD:AAO3409	this study	LepF1/LepR1
<i>Xanthocotelles fritzi</i>	CCDB-30346-C11	BOLD:ADL3417	this study	LepF1/LepR1
<i>Xanthocotelles sicheli</i>	CCDB-30384-H10	BOLD:ADQ9224	this study	C_LepFolF/C_LepFolR

<sup>1</sup>The generic classification of Colletinae adopted herein follows Toro and Cabezas (1977, 1978).

<sup>2</sup>Species originally identified as *C. mitchelli* Stephen which is a junior synonym of *C. speculiferus* according to Hall et al. (2016).

<sup>3</sup>Sequence generously provided to us by Julio Genaro.

<sup>4</sup>Sequence generously provided to us by Berry Brosi.

**Table S4.** Sequences of the primers used in the PCR amplifications. 28S: 28S rRNA large subunit; COI: cytochrome c oxidase subunit 1; EF1a: elongation factor-1 $\alpha$  copy F2; opsin: long wavelength rhodopsin; pol II: RNA polymerase II.

Locus	Primer	Sequence	Reference
28S	Bel28S-For	5'-AGAGAGAGTTCAAGAGTACGTG-3'	Belshaw and Quicke, 1997
	28SD4-Rev	5'-GTTACACACTCCTTAGCGGA-3'	Danforth et al., 2006
COI	C_LepFolF	5'-ATT CAA CCA ATC ATA AAG ATA TTG G-3'	Heber et al., 2004
	C_LepFolR	5'-TAAACTTCTGGATGTCCAAAAAATCA-3'	Heber et al., 2004
	LepF1	5'-ATTCAACCAATCATAAAGATATTGG-3'	Heber et al., 2004
	LepR1	5'-TAAACTTCTGGATGTCCAAAAAATCA-3'	Heber et al., 2004
	RonMWASPdeg_t1	5'-TGTAACGACGGCCAGTGGWTCWCCWGATATAKCWTTTCC-3'	Smith et al., 2009
EF1a	HaF2For1	5'-GGGYAAAGGWTCTTCAARTATGC-3'	Danforth et al., 1999
	F2-rev1	5'-AATCAGCAGCACCTTTAGGTGG-3'	Danforth et al., 1999
opsin	Opsin-For	5'-AATTGCTATTAYGARACNTGGGT-3'	Mardulyn and Whitfield, 1999
	Opsin-Rev	5'-ATANGGNGTCCANGCCATGAACCA-3'	Mardulyn and Whitfield, 1999
pol II	polfor2a	5'-AAYAARCCVGTATGGGTATTGTRCA-3'	Danforth et al., 2006
	polrev2a	5'-AGRTANGARTTCTCRACGAATCCTCT-3'	Danforth et al., 2006
wingless	Wg-Collet-For	5'-CACGTGTCBTCBGRGATGMGRSAGGA-3'	Almeida and Danforth, 2009
	Lep-Wg2a-Rev	5'-ACT ICGCARCACCARTGGAATGTRCA-3'	Brower and DeSalle, 1998

**Table S5.** Species groups of *Colletes* in the Neotropics with an updated checklist of the 123 species distributed in the region. Groups marked with an asterisk (\*) are exclusively Neotropical and are proposed herein for the first time; the others were originally proposed for the Nearctic by Stephen (1954). Placement of species marked with a question mark (?) is only tentative.

Species groups/species	Distribution
<b><i>COLLETES ALOCOCHILA</i> GROUP*</b>	
<b><i>Colletes alocochila</i> Moure, 1956</b> <i>Colletes alocochila</i> Moure, 1956: 208	Chile, Peru
<b><i>Colletes atacamensis</i> Janvier, 1955</b> <i>Colletes atacamensis</i> Janvier, 1955: 316 <i>Colletes atacamensis</i> Moure, 1956: 204 <i>Colletes atacamanus</i> Moure, 1997: 513	Chile, Peru
<b><i>Colletes nigropilosus</i> Ferrari, 2017</b> <i>Colletes nigropilosus</i> Ferrari, 2017: 94	Chile
<b><i>Colletes nitidicollis</i> Friese, 1900</b> <i>Colletes nitidicollis</i> Friese, 1900: 182	Bolivia, Peru
<b><i>Colletes simulatus</i> Ferrari, 2017</b> <i>Colletes simulatus</i> Ferrari, 2017: 107	Chile
<b><i>Colletes striginasis</i> Vachal, 1909</b> <i>Colletes striginasis</i> Vachal, 1909: 48	Peru
<b><i>Colletes ursinus</i> Smith, 1853?</b> <i>Colletes ursina</i> Smith, 1853: 5	Colombia
<b><i>COLLETES AMERICANUS</i> GROUP</b>	
<b><i>Colletes tzotzilis</i> Balboa and Ayala, 2017</b> <i>Colletes tzotzilis</i> Balboa and Ayala, 2017: 402	Mexico
<b><i>Colletes volsellatus</i> Metz, 1910</b> <i>Colletes volsellata</i> Metz, 1910: 197	Mexico
<b><i>COLLETES ARTHURI</i> GROUP*</b>	
<b><i>Colletes arthuri</i> Ferrari, 2017</b> <i>Colletes arthuri</i> Ferrari, 2017: 18	Chile
<b><i>COLLETES ATRIPES</i> GROUP*</b>	
<b><i>Colletes atripes</i> Smith, 1854</b> <i>Colletes dimidiata</i> Spinola, 1851: 225 <i>Colletes atripes</i> Smith, 1854: 418	Argentina, Chile
<b><i>Colletes cognatus</i> Spinola, 1851</b> <i>Colletes cognata</i> Spinola, 1851: 223	Argentina, Chile
<b><i>Colletes coquimbensis</i> Ferrari, 2017</b> <i>Colletes coquimbensis</i> Ferrari, 2017: 40	Chile
<b><i>Colletes costaricensis</i> Friese, 1916?</b> <i>Colletes costaricensis</i> Friese, 1916: 302	Colombia, Costa Rica, Ecuador, Mexico

<b><i>Colletes mastochila</i> Moure, 1956</b> <i>Colletes mastochila</i> Moure, 1956: 206	Argentina, Bolivia, Chile, Peru
<b>COLLETES BICOLOR GROUP*</b>	
<b><i>Colletes bicolor</i> Smith, 1879</b> <i>Colletes bicolor</i> Smith, 1879: 3 <i>Biglossa andina</i> Jörgensen, 1909: 221	Argentina, Chile
<b><i>Colletes clematidis</i> Jörgensen, 1912</b> <i>Colletes clematidis</i> Jörgensen, 1912: 93	Argentina
<b><i>Colletes cyaniventris</i> Spinola, 1851</b> <i>Colletes cyani-ventris</i> Spinola, 1851: 224 <i>Colletes atripilis</i> Vachal, 1909: 55	Argentina, Chile
<b><i>Colletes nigrutilus</i> Friese, 1910</b> <i>Colletes nigrutilus</i> Friese, 1910: 645	Argentina, Chile
<b><i>Colletes weiskei</i> Friese, 1912?</b> <i>Colletes weiskei</i> Friese, 1912: 364	Argentina
<b>COLLETES BOMBIFORMIS GROUP*</b>	
<b><i>Colletes aethiops</i> Cresson, 1868</b> <i>Colletes aethiops</i> Cresson, 1868: 169	Mexico, Panama
<b><i>Colletes bombiformis</i> Metz, 1910</b> <i>Colletes bombiformis</i> Metz, 1910: 206	Mexico
<b>COLLETES CONSORS GROUP</b>	
<b><i>Colletes guadalajarensis</i> Metz, 1910</b> <i>Colletes guadalajarensis</i> Metz, 1910: 198	Mexico
<b>COLLETES CHUSMIZA GROUP*</b>	
<b><i>Colletes chusmiza</i> Rojas and Toro, 1993</b> <i>Colletes chusmiza</i> Rojas and Toro, 1993: 83	Chile
<b><i>Colletes flaminii</i> Moure, 1956</b> <i>Colletes flaminii</i> Moure, 1956: 203	Argentina, Chile
<b><i>Colletes fulvipes</i> Spinola, 1851</b> <i>Colletes fulvipes</i> Spinola, 1851: 225	Argentina, Chile
<b><i>Colletes guanta</i> Rojas and Toro, 1993</b> <i>Colletes guanta</i> Rojas and Toro, 1993: 84	Chile
<b><i>Colletes quelu</i> Rojas and Toro, 1993</b> <i>Colletes quelu</i> Rojas and Toro, 1993: 85	Chile
<b><i>Colletes vicugnensis</i> Rojas &amp; Toro, 1993</b> <i>Colletes vicugnensis</i> Rojas & Toro, 1993: 85	Chile
<b>COLLETES CYANEUS GROUP*</b>	
<b><i>Colletes azureus</i> Friese, 1912?</b> <i>Colletes azureus</i> Friese, 1912: 365	Argentina



<b><i>Colletes brethesi</i> Jörgensen, 1912</b>	Argentina
<i>Colletes brethesi</i> Jörgensen, 1912: 94	
<b><i>Colletes chalybaeus</i> Friese, 1910</b>	Argentina
<i>Colletes chalybaeus</i> Friese, 1910: 646	
<b><i>Colletes cyanescens</i> (Haliday, 1836)</b>	Argentina, Chile
<i>Andrena cyanescens</i> Haliday, 1836: 321	
<i>Colletes semi-nitida</i> Spinola, 1851: 225	
<i>Colletes viridans</i> Vachal, 1909: 55	
<b><i>Colletes cyaneus</i> Holmberg, 1903</b>	Argentina, Brazil
<i>Colletes cyaneus</i> Holmberg, 1903: 468	
<b><i>Colletes michenerianus</i> Moure, 1956</b>	Brazil
<i>Colletes micheneriana</i> Moure, 1956: 201	
<b><i>Colletes musculus</i> Friese, 1910</b>	Argentina, Chile
<i>Colletes musculus</i> Friese, 1910: 647	
<i>Colletes ciliatus</i> Friese, 1910: 647	
<i>Colletes biciliatus</i> Cockerell, 1918: 138	
<i>Colletes chubutensis</i> Cockerell, 1918: 137	
<i>Colletes polynidus</i> Stephen, 1953: 40	
<b><i>Colletes vachali</i> Jörgensen, 1912</b>	Argentina
<i>Colletes vachali</i> Joergensen, 1912: 93	
<b><i>Colletes virgatus</i> Vachal, 1904?</b>	Argentina
<i>Colletes virgatus</i> Vachal, 1904: 26	
<b>COLLETES DALEAE GROUP</b>	
<b><i>Colletes algorobiae</i> Cockerell, 1900?</b>	Mexico, USA
<i>Colletes algorobiae</i> Cockerell, 1900: 244	
<b>COLLETES FURFURACEUS GROUP*</b>	
<b><i>Colletes clarus</i> Jörgensen, 1912</b>	Argentina
<i>Colletes clarus</i> Jörgensen, 1912: 98	
<b><i>Colletes furfuraceus</i> Holmberg, 1886</b>	Argentina, Brazil, Paraguay
<i>Colletes furfuracea</i> Holmberg, 1886: 183	
<b><i>Colletes steinbachi</i> Friese, 1910?</b>	Argentina
<i>Colletes steinbachi</i> Friese, 1910: 651	
<b>COLLETES GILVUS GROUP*</b>	
<b><i>Colletes gilvus</i> Vachal, 1909</b>	Chile
<i>Colletes gilvus</i> Vachal, 1909: 56	
<i>Colletes tomentosus</i> Friese, 1910: 648	
<b><i>Colletes kuhlmanni</i> Ferrari, 2017</b>	Chile
<i>Colletes kuhlmanni</i> Ferrari, 2017: 70	
<b><i>Colletes lycii</i> Jörgensen, 1912</b>	Argentina
<i>Colletes lycii</i> Jörgensen, 1912: 96	
<b><i>Colletes mimincus</i> Cockerell, 1914</b>	Peru
<i>Colletes miminca</i> Cockerell, 1914: 328	

<b><i>Colletes murinus</i> Friese, 1900</b>	Chile, Peru
<i>Colletes murinus</i> Friese, 1900: 184	
<b><i>Colletes peruvicus</i> Cockerell, 1913</b>	Peru
<i>Colletes lycii peruvicus</i> Cockerell, 1913: 185	
<b><i>Colletes sulcatus</i> Vachal, 1909</b>	Chile
<i>Colletes sulcatus</i> Vachal, 1909: 58	
<i>Colletes araucariae</i> Friese, 1910: 649	
<b><i>Colletes toroi</i> Ferrari, 2017</b>	Chile
<i>Colletes toroi</i> Ferrari, 2017: 113	
 <b>COLLETES HYALINUS GROUP</b>	
<b><i>Colletes hicaco</i> Genaro, 2003</b>	Cuba
<i>Colletes hicaco</i> Genaro, 2003: 54	
 <b>COLLETES INTERMIXTUS GROUP</b>	
<b><i>Colletes dilatatus</i> Metz, 1910</b>	Mexico
<i>Colletes dilatata</i> Metz, 1910: 194	
<b><i>Colletes jobeli</i> Balboa and Ayala, 2017</b>	Mexico
<i>Colletes jobeli</i> Balboa and Ayala, 2017: 405	
<b><i>Colletes nigerrima</i> Balboa and Ayala, 2017</b>	Mexico
<i>Colletes nigerrima</i> Balboa and Ayala, 2017: 413	
<b><i>Colletes recurvatus</i> Metz, 1910</b>	Mexico
<i>Colletes recurvata</i> Metz, 1910: 192	
 <b>COLLETES KERRI GROUP*</b>	
<b><i>Colletes ferenudus</i> Ferrari, 2019</b>	Brazil
<i>Colletes ferenudus</i> Ferrari, 2019: 25	
<b><i>Colletes kerri</i> Moure, 1956</b>	Brazil
<i>Colletes kerri</i> Moure, 1956: 197	
 <b>COLLETES LATITARSIS GROUP</b>	
<b><i>Colletes chiapensis</i> Balboa and Ayala, 2017?</b>	Guatemala, Mexico
<i>Colletes chiapensis</i> Balboa and Ayala, 2017: 409	
<b><i>Colletes granpiedrensis</i> Genaro, 2001</b>	Cuba
<i>Colletes granpiedrensis</i> Genaro, 2001: 1028	
<b><i>Colletes isthmicus</i> Swenk, 1930?</b>	Costa Rica, Panama
<i>Colletes isthmicus</i> Swenk, 1930: 219	
<b><i>Colletes mexicanus</i> Cresson, 1868?</b>	Costa Rica, Mexico
<i>Colletes mexicana</i> Cresson, 1868: 170	
<b><i>Colletes panamensis</i> Michener, 1954</b>	Panama
<i>Colletes panamensis</i> Michener, 1954: 20	
<b><i>Colletes rohweri</i> Cockerell, 1918?</b>	Costa Rica, Ecuador
<i>Colletes rohweri</i> Cockerell, 1918: 206	
<b><i>Colletes solari</i> Balboa and Ayala, 2017</b>	Mexico
<i>Colletes solari</i> Balboa and Ayala, 2017: 418	

***Colletes submarginatus* Cresson, 1865**

*Colletes submarginata* Cresson, 1865: 167

Bahamas, Cuba

**COLLETES LONGICEPS GROUP\***

***Colletes longiceps* Friese, 1910**

*Colletes longiceps* Friese, 1910: 649

Argentina, Chile

***Colletes mourei* Kuhlmann, 1999?**

*Colletes similis* Jörgensen, 1912: 96

*Colletes mourei* Kuhlmann, 1999: 78

Argentina

*Colletes desantisi* Moure and Urban, 2002: 9

***Colletes neoqueenensis* Friese, 1910**

*Colletes neoqueenensis* Friese, 1910: 649

Argentina

***Colletes tingoensis* Cockerell, 1926?**

*Colletes tingoensis* Cockerell, 1926: 302

Peru

**COLLETES ORNATUS GROUP\***

***Colletes ornatus* Schrottky, 1902**

*Colletes ornatus* Schrottky, 1902: 345

Argentina, Brazil, Paraguay

***Colletes quadrigenis* Vachal, 1909**

*Colletes quadrigenis* Vachal, 1909: 51

Argentina

**COLLETES PATAGONICUS GROUP\***

***Colletes flavipilosus* Ferrari, 2017**

*Colletes flavipilosus* Ferrari, 2017: 56

Chile

***Colletes lucens* Vachal, 1909**

*Colletes lucens* Vachal, 1909: 57

Chile

*Colletes laticeps* Friese, 1910: 651

***Colletes patagonicus* Schrottky, 1907**

*Colletes patagonicus* Schrottky, 1907: 7

Argentina, Chile

*Colletes rhodaspis* Cockerell, 1909: 397

*Colletes rufosignatus* Cockerell, 1918: 138

*Colletes campoi* Herbst, 1920: 8

**COLLETES PETROPOLITANUS GROUP\***

***Colletes eupogonites* Moure, 1949**

*Colletes eupogonites* Moure, 1949: 439

Argentina

***Colletes hawking* Ferrari, 2019**

*Colletes hawking* Ferrari, 2019: 36

Brazil

***Colletes joergenseni* Friese, 1910**

*Colletes joergenseni* Friese, 1910: 650

Argentina

***Colletes montefragus* Raw, 1984**

*Colletes montefragus* Raw, 1984: 492

Jamaica

***Colletes motaguensis* Cockerell, 1912?**

*Colletes motaguensis* Cockerell, 1912: 564

Guatemala

<b><i>Colletes nautlanus</i> Cockerell, 1899?</b>	Mexico
<i>Colletes nautlanus</i> Cockerell, 1899: 154	
<b><i>Colletes petropolitanus</i> Dalla Torre, 1896</b>	Argentina, Bolivia, Brazil, Paraguay, Peru
<i>Colletes senilis</i> Smith, 1879: 3	
<i>Colletes petropolitanus</i> Dalla Torre, 1896: 43	
<i>Colletes catulus</i> Vachal, 1904: 26	
<i>Colletes inflatus</i> Vachal, 1909: 49	
<i>Colletes speculiventris</i> Cockerell, 1917: 438	
<b><i>Colletes schrottky</i> Joergensen, 1912</b>	Argentina
<i>Colletes schrottky</i> Joergensen, 1912: 97	
<b>COLLETES PRODUCTUS GROUP</b>	
<b><i>Colletes guatemalensis</i> Balboa and Ayala, 2017</b>	Guatemala
<i>Colletes guatemalensis</i> Balboa and Ayala, 2017: 407	
<b><i>Colletes vandylei</i> Timberlakei, 1951?</b>	Mexico, USA
<i>Colletes vandylei</i> Timberlakei, 1951: 200	
<b>COLLETES RUFIPES GROUP*</b>	
<b><i>Colletes altimontanus</i> Ferrari and Silveira, 2015</b>	Brazil
<i>Colletes altimontanus</i> Ferrari and Silveira, 2015: 249	
<b><i>Colletes brevinodis</i> Vachal, 1909</b>	Bolivia
<i>Colletes brevinodis</i> Vachal, 1909: 52	
<b><i>Colletes chicoi</i> Ferrari, 2019</b>	Brazil
<i>Colletes chicoi</i> Ferrari, 2019: 18	
<b><i>Colletes flagellaris</i> Ferrari, 2019</b>	Brazil
<i>Colletes flagellaris</i> Ferrari, 2019: 28	
<b><i>Colletes imbricatus</i> Ferrari, 2019</b>	Brazil
<i>Colletes imbricatus</i> Ferrari, 2019: 40	
<b><i>Colletes meridionalis</i> Schrottky, 1902</b>	Brazil
<i>Colletes rufipes meridionalis</i> Schrottky, 1902: 345	
<i>Colletes extensicornis</i> Vachal, 1909: 53	
<b><i>Colletes pampeanus</i> Ferrari, 2019</b>	Brazil
<i>Colletes pampeanus</i> Ferrari, 2019: 57	
<b><i>Colletes rufipes</i> Smith, 1879</b>	Brazil
<i>Colletes rufipes</i> Smith, 1879: 3	
<b><i>Colletes sertanicola</i> Ferrari, 2019</b>	Brazil
<i>Colletes sertanicola</i> Ferrari, 2019: 73	
<b><i>Colletes sexangulus</i> Ferrari, 2019</b>	Brazil
<i>Colletes sexangulus</i> Ferrari, 2019: 76	
<b>COLLETES RUGICOLLIS GROUP*</b>	
<b><i>Colletes argentinus</i> Friese, 1908</b>	Argentina, Brazil, Uruguay
<i>Colletes argentinus</i> Friese, 1908: 10	
<b><i>Colletes nigrior</i> Michener, 1954</b>	Costa Rica, Guatemala, Mexico, Panama
<i>Colletes rugicollis nigrior</i> Michener, 1954: 17	

***Colletes rugicollis* Friese, 1900**

*Colletes rugicollis* Friese, 1900: 183

*Colletes punctatissimus* Schrottky, 1902: 347

Bolivia, Brazil, Peru

**COLLETES SIMULANS GROUP**

***Colletes aztecus* Cresson, 1868**

*Colletes azteca* Cresson, 1868: 169

Mexico

***Colletes delicatus* Metz, 1910**

*Colletes delicata* Metz, 1910: 203

Mexico

***Colletes isabellae* Balboa and Ayala, 2017**

*Colletes isabellae* Balboa and Ayala, 2017: 416

Mexico

***Colletes jaliscoensis* Balboa and Ayala, 2017**

*Colletes jaliscoensis* Balboa and Ayala, 2017: 411

Mexico

***Colletes lineatus* Metz, 1910**

*Colletes lineatus* Metz, 1910: 196

Mexico, USA

***Colletes macconnelli* Metz, 1910**

*Colletes macconnelli* Metz, 1910: 201

Mexico

***Colletes moctezumensis* Metz, 1910**

*Colletes moctezumensis* Metz, 1910: 200

Mexico

***Colletes rutilans* Vachal, 1909**

*Colletes rutilans* Vachal, 1909: 52

Chile, Colombia, Ecuador, Peru

***Colletes subdilatatus* Metz, 1910?**

*Colletes subdilatatus* Metz, 1910: 204

Mexico

**COLLETES SPILOPTERUS GROUP\***

***Colletes punctipennis* Cresson, 1868?**

*Colletes punctipennis* Cresson, 1868: 169

Costa Rica, El Salvador, Guatemala, Mexico

***Colletes spilopterus* Cockerell, 1917**

*Colletes spiloptera* Cockerell, 1917: 363

Costa Rica, Panama, Mexico

*Colletes maculipennis* Friese, 1921: 83

**COLLETES VENTRICARINATUS GROUP\***

***Colletes ventricarinatus* Ferrari, 2017**

*Colletes ventricarinatus* Ferrari, 2017: 116

Chile

**SPECIES OF DOUBTFUL PLACEMENT:**

***Colletes antiguensis* Cockerell, 1912**

*Colletes antiguensis* Cockerell, 1912: 565

Guatemala

***Colletes bruneri* Schenk, 1904**

*Colletes bruneri* Schenk, 1904: 77

Costa Rica, Mexico

***Colletes capitatus* Metz, 1910**

*Colletes capitata* Metz, 1910: 204

Mexico

***Colletes frontalis* Metz, 1910**

*Colletes frontalis* Metz, 1910: 207

Mexico

<b><i>Colletes grisellus</i> Michener, 1989</b>	Mexico
<i>Colletes griseus</i> Smith, 1879: 2	
<i>Colletes grisellus</i> Michener, 1989: 703	
<b><i>Colletes griseus</i> (Westwood, 1875)</b>	Mexico
<i>Monia grisea</i> Westwood, 1875: 22	
<b><i>Colletes intricatus</i> Smith, 1879</b>	Mexico
<i>Colletes intricatus</i> Smith, 1879: 2	
<b><i>Colletes mexicanicola</i> Strand, 1919</b>	Mexico
<i>Colletes mexicanicola</i> Strand, 1919: 19	
<b><i>Colletes mexiconis</i> Strand, 1919</b>	Mexico
<i>Colletes mexiconis</i> Strand, 1919 : 14	
<b><i>Colletes niger</i> Swenk, 1904</b>	Costa Rica
<i>Colletes niger</i> Swenk, 1904: 76	
<b><i>Colletes nitidillabris</i> Strand, 1919</b>	Mexico
<i>Colletes nitidillabris</i> Strand, 1919: 22	
<b><i>Colletes perplexus</i> Smith, 1879</b>	Honduras, Mexico
<i>Colletes perplexus</i> Smith, 1879: 1	
<b><i>Colletes pinnatus</i> Vachal, 1909</b>	Argentina
<i>Colletes pinnatus</i> Vachal, 1909: 51	
<b><i>Colletes tehuacanus</i> Strand, 1919</b>	Mexico
<i>Colletes tehuacanus</i> Strand, 1919: 13	

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**Table S6.** Comparison between the intrageneric classification of *Colletes* according to Kuhlmann et al. (2009) and the one proposed in the present study. Groups marked with an asterisk (\*) were not available for our phylogenetic analysis. All Neotropical groups are here being proposed the first time (see Table S5). For species composition of the Nearctic and Old World groups consult Stephen (1954) and Kuhlman (2000, 2014), respectively.

Subgenera	Kuhlmann et al. (2009)	This study
<b><i>Albocolletes</i> Warncke, 1978<sup>1</sup></b> type species: <i>C. albomaculatus</i> (Lucas, 1849)	<i>albomaculatus</i> group	<i>albomaculatus</i> group (Palearctic)
<b><i>Colletes</i> s.str. Latreille, 1802</b> type species: <i>C. succinctus</i> (Linnaeus, 1758)	<i>anchusae</i> group <i>meyeri</i> group <i>succinctus</i> group	<i>clypearis</i> group (Palearctic/Indo-Malay) <i>conradti</i> group (Palearctic) <i>graeffei</i> group (Palearctic) <i>marginatus</i> group (Palearctic/Indo-Malay) <i>mixtus</i> group <sup>2</sup> (Palearctic) <i>roborovskyi</i> group <sup>2</sup> (Palearctic) <i>simulans</i> group (Nearctic) <i>succinctus</i> group (Palearctic/Indo-Malay) Possibly including: <i>meyeri</i> group* (Palearctic)
<b><i>Denticolletes</i> Noskiewicz, 1936</b> type species: <i>C. graeffei</i> Alfken, 1900	<i>graeffei</i> group	Synonym of <i>Colletes</i> ( <i>Colletes</i> s.str.)
<b><i>Elecolletes</i> Warncke, 1978</b> type species: <i>C. elegans</i> Noskiewicz, 1936	<i>carinatus</i> group <i>caspicus</i> group <i>hylaeiformis</i> group <i>nigricans</i> group <i>squamosus</i> group	<i>carinatus</i> group (Palearctic) <i>caspicus</i> group (Palearctic/Indo-Malay) <i>hylaeiformis</i> group (Palearctic) <i>nigricans</i> group (Palearctic) <i>squamosus</i> group (Palearctic/Indo-Malay)

***Nanocolletes* Warncke, 1978**

type species: *C. nanus* Friese, 1898

*diodontus* group

*foveolaris* group

*nanus* group

*africanus* group\* (Afrotropical)

*antecessus* group (Afrotropical)

*capensis* group (Afrotropical)

*claripes* group (Afrotropical)

*diondontus* group\* (Palearctic)

*fasciatus* group (Afrotropical)

*formosus* group (Palearctic)

*foveolaris* group (Palearctic/Indo-Malay)

*fusconotus* group (Afrotropical)

*inaequalis* group (Nearctic)

*lacunatus* group (Palearctic/Indo-Malay)

*malmus* group (Afrotropical)

*nanus* group (Palearctic/Indo-Malay)

*rufitarsis* group (Afrotropical)

*C. reginae* Cockerell\* (Afrotropical)

Possibly including:

*microdontus* group\* (Afrotropical)

*rufotibialis* group\* (Afrotropical)

***Pachycolletes* Bischoff in Stoeckhert, 1954<sup>3</sup>**

type species: *C. cunicularius* (Linnaeus, 1761)

*acutus* group

*cariniger* group

*cunicularius* group

*formosus* group

*lacunatus* group

*americanus* group (Nearctic)

*bombiformis* group (Neotropical)

*cariniger* group\* (Palearctic)

*consors* group (Nearctic)

*cunicularius* group (Palearctic/Indo-Malay)

*hyalinus* group (Nearctic)

*intermixtus* group (Nearctic)

*latitarsis* group (Nearctic)

*nudus* group (Nearctic)

*petropolitanus* group (Neotropical)

*productus* group (Nearctic)  
*robertsonii* group (Nearctic)  
*rugicollis* group (Neotropical)  
*willistoni* group (Nearctic)  
 Possibly including:  
*spilopterus* group\* (Neotropical)  
*C. antiguensis* Cockerell\* (Neotropical)  
*C. bruneri* Swenk\* (Neotropical)  
*C. capitatus* Metz\* (Neotropical)  
*C. frontalis* Metz\* (Neotropical)  
*C. grisellus* Michener\* (Neotropical)  
*C. griseus* (Westwood)\* (Neotropical)  
*C. intricatus* Smith\* (Neotropical)  
*C. mexicanicola* Strand\* (Neotropical)  
*C. mexiconis* Strand\* (Neotropical)  
*C. niger* Swenk\* (Neotropical)  
*C. nitidillabris* Strand\* (Neotropical)  
*C. perplexus* Smith\* (Neotropical)  
*C. tehuacanus* Strand\* (Neotropical)

***Rhinocolletes* Cockerell, 1910**

type species: *C. natusus* Smith, 1853

*nasutus* group

*anchusae* group (Palearctic)  
*fodiens* group (Palearctic)  
*nasutus* group (Palearctic)  
 Possibly including:  
*senilis* group\* (Palearctic)  
*turdus* group\* (Palearctic)  
*uralensis* group\* (Palearctic)

***Simcolletes* Warncke, 1978**

type species: *C. similis* Schenk, 1853

*clypearis* group  
*conradti* group  
*fodiens* group  
*marginatus* group  
*senilis* group  
*simulans* group  
*uralensis* group  
*tardus* group

Synonym of *Rhinocolletes*

**New subgenus 1**

Not applicable

*arthuri* group (Neotropical)  
*alocochila* group (Neotropical)  
*atripes* group (Neotropical)  
*bicolor* group (Neotropical)  
*cyaneus* group (Neotropical)  
*chusmiza* group (Neotropical)  
*furfuraceus* group (Neotropical)  
*gilvus* group (Neotropical)  
*longiceps* group\* (Neotropical)  
*kerri* group (Neotropical)  
*ornatus* group\* (Neotropical)  
*patagonicus* group (Neotropical)  
*rufipes* group (Neotropical)  
*ventricarinatus* group\* (Neotropical)  
Possibly including:  
*C. pinnatus* Vachal\* (Neotropical)

**New subgenus 2**

Not applicable

*compactus* group (Nearctic)  
*daleae* group (Nearctic)

*Incertae sedis*

<i>arenarius</i> group	<i>acutus</i> group (Palearctic)
<i>flavicornis</i> group	<i>aestivalis</i> group* (Nearctic)
<i>C. dorni</i> Kuhlmann	<i>arenarius</i> group* (Palearctic)
<i>C. dugeonii</i> Bingham	<i>aridus</i> group* (Nearctic)
<i>C. sichuanensis</i>	<i>ciliatus</i> group* (Nearctic)
Kuhlmann	<i>flavicornis</i> group* (Palearctic)
<i>C. wacki</i> Kuhlmann	<i>longifascies</i> group* (Nearctic)
	<i>titusensis</i> group* (Nearctic)
	<i>C. dorni</i> *
	<i>C. dugeonii</i> *
	<i>C. sichuanensis</i> *
	<i>C. wacki</i> *

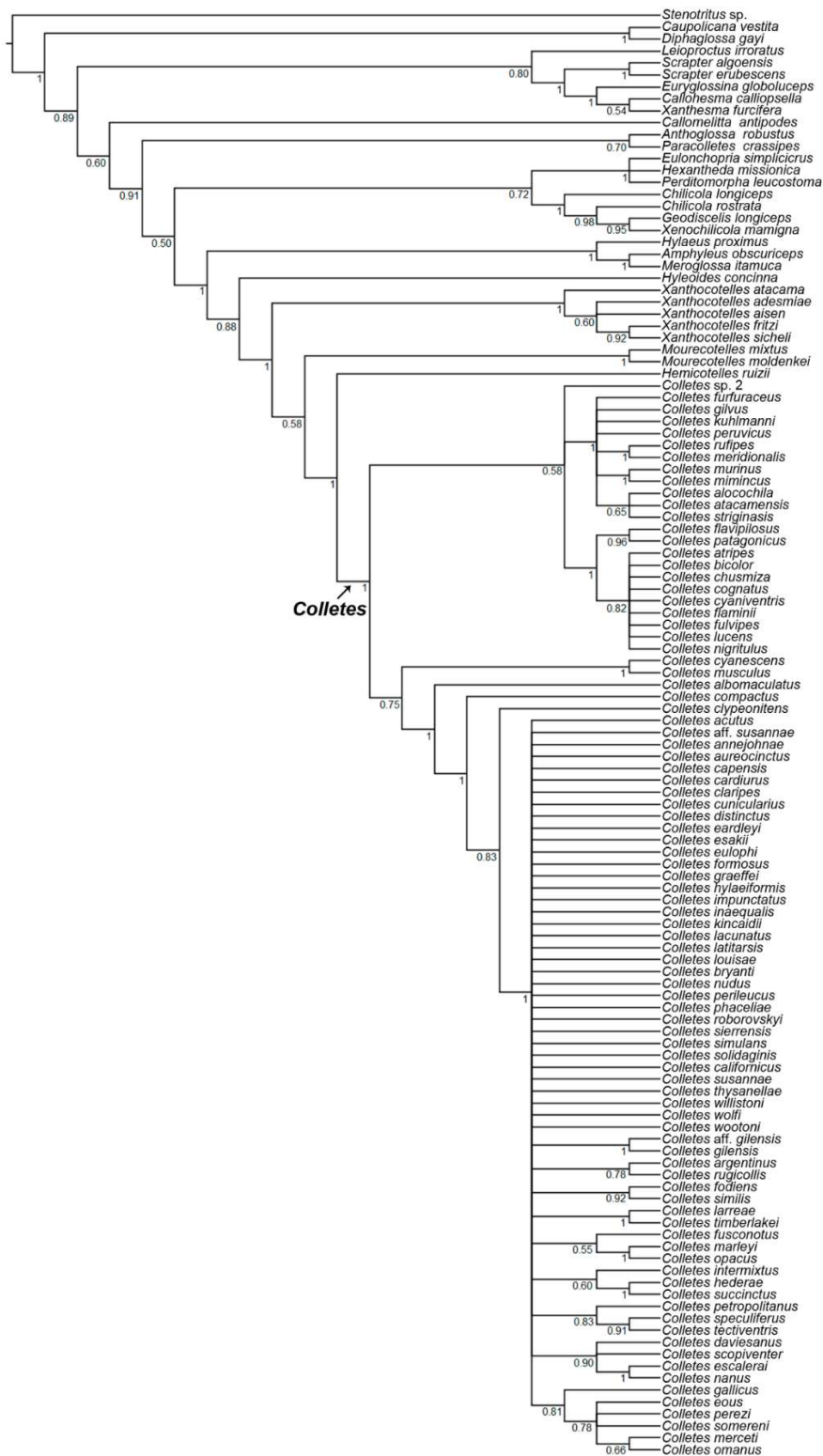
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<sup>1</sup>Even though Kuhlmann et al. (2009) included *Albocolletes* in their classification, the authors indicated that it was probably a synonym of *Rhinocolletes*.

<sup>2</sup>Groups that were placed within a separate, unnamed subgenus by Kuhlmann et al. (2009).

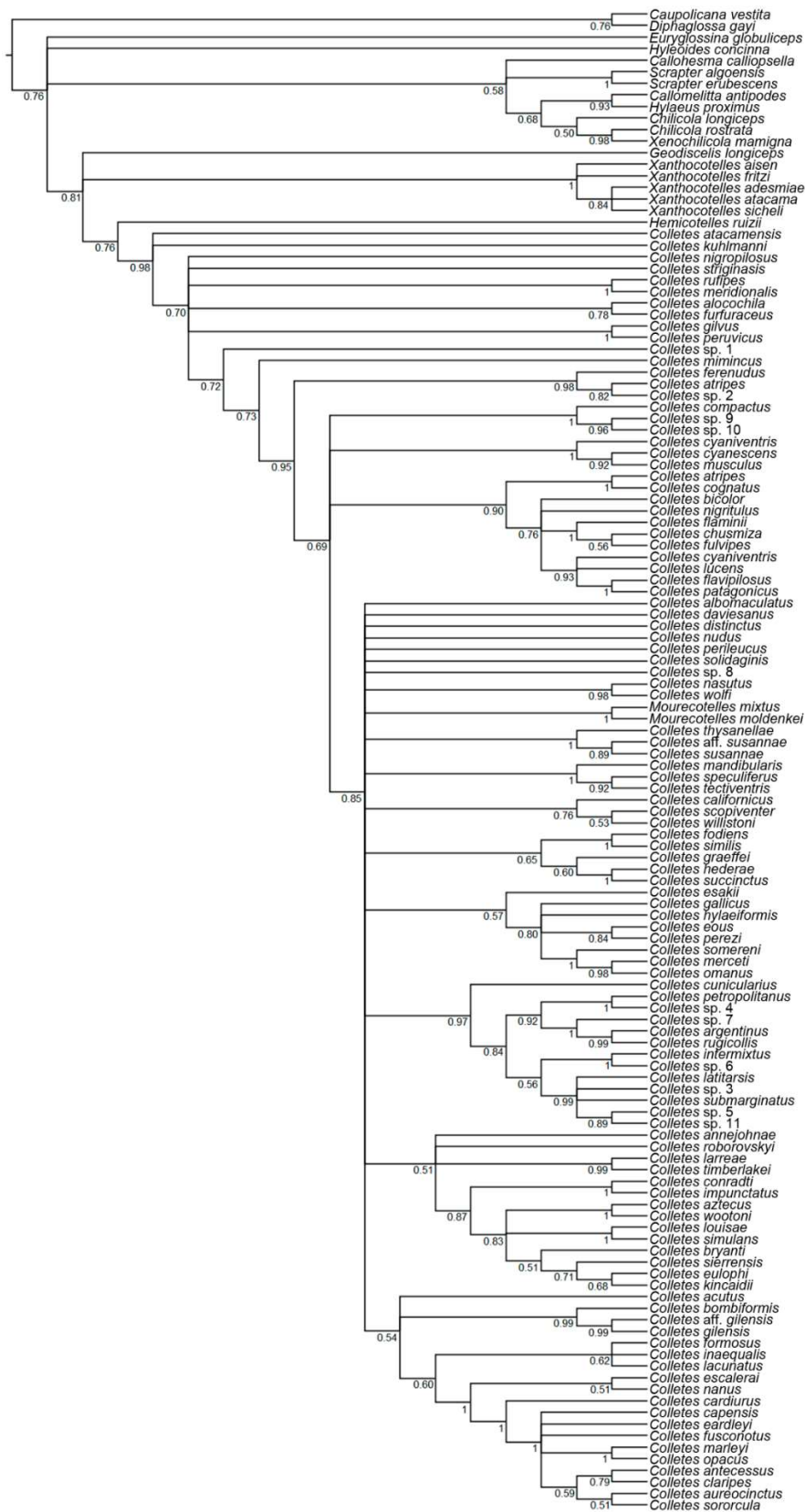
<sup>3</sup>Potentially a synonym of *Ptilopoda* Friese, 1921.

## Appendix II: Supplementary figures

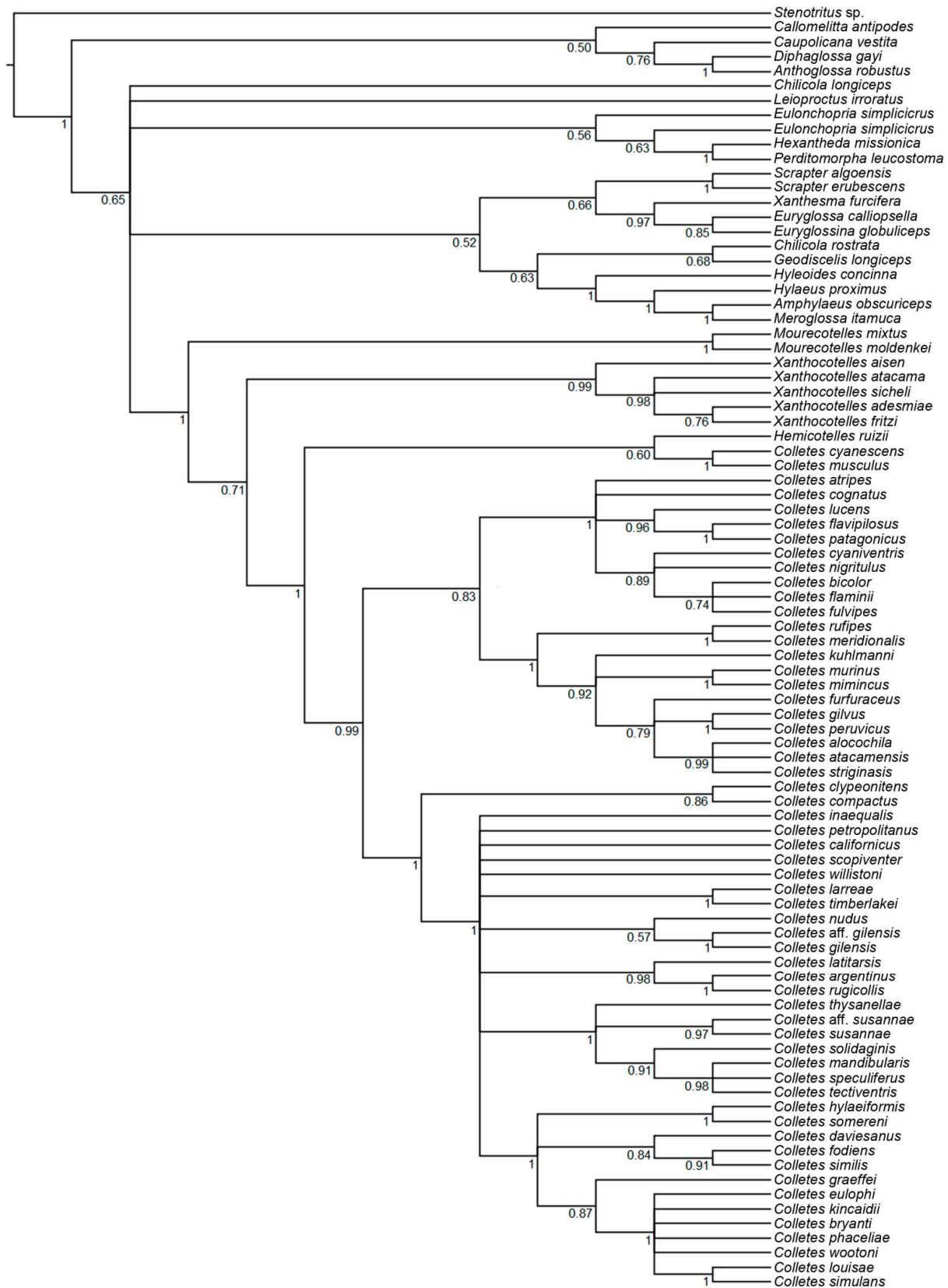


**Figure S1.** Bayesian tree obtained through analysis of the 28S sequence data in MrBayes. Numbers below internal branches are posterior probabilities of the corresponding clades.

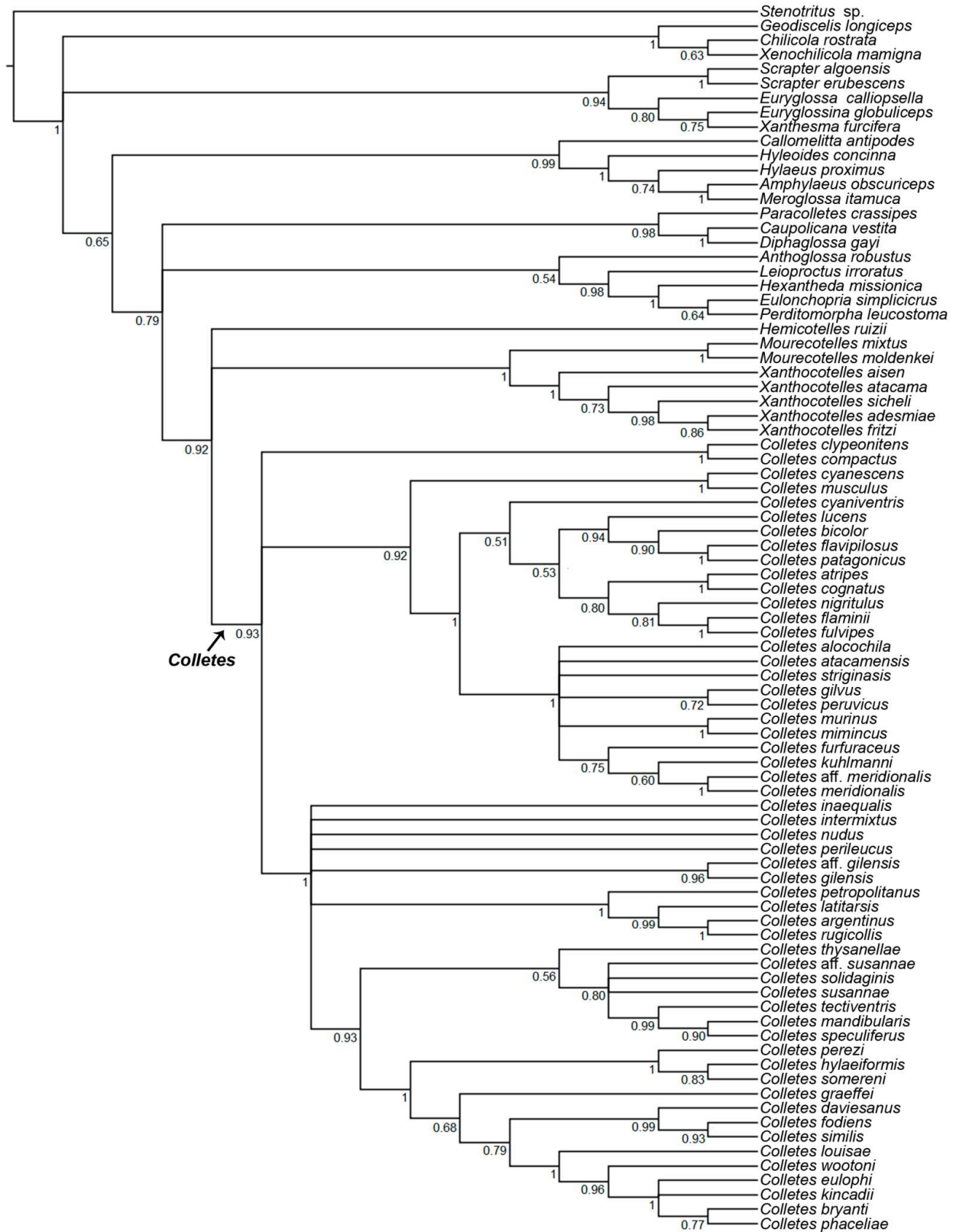




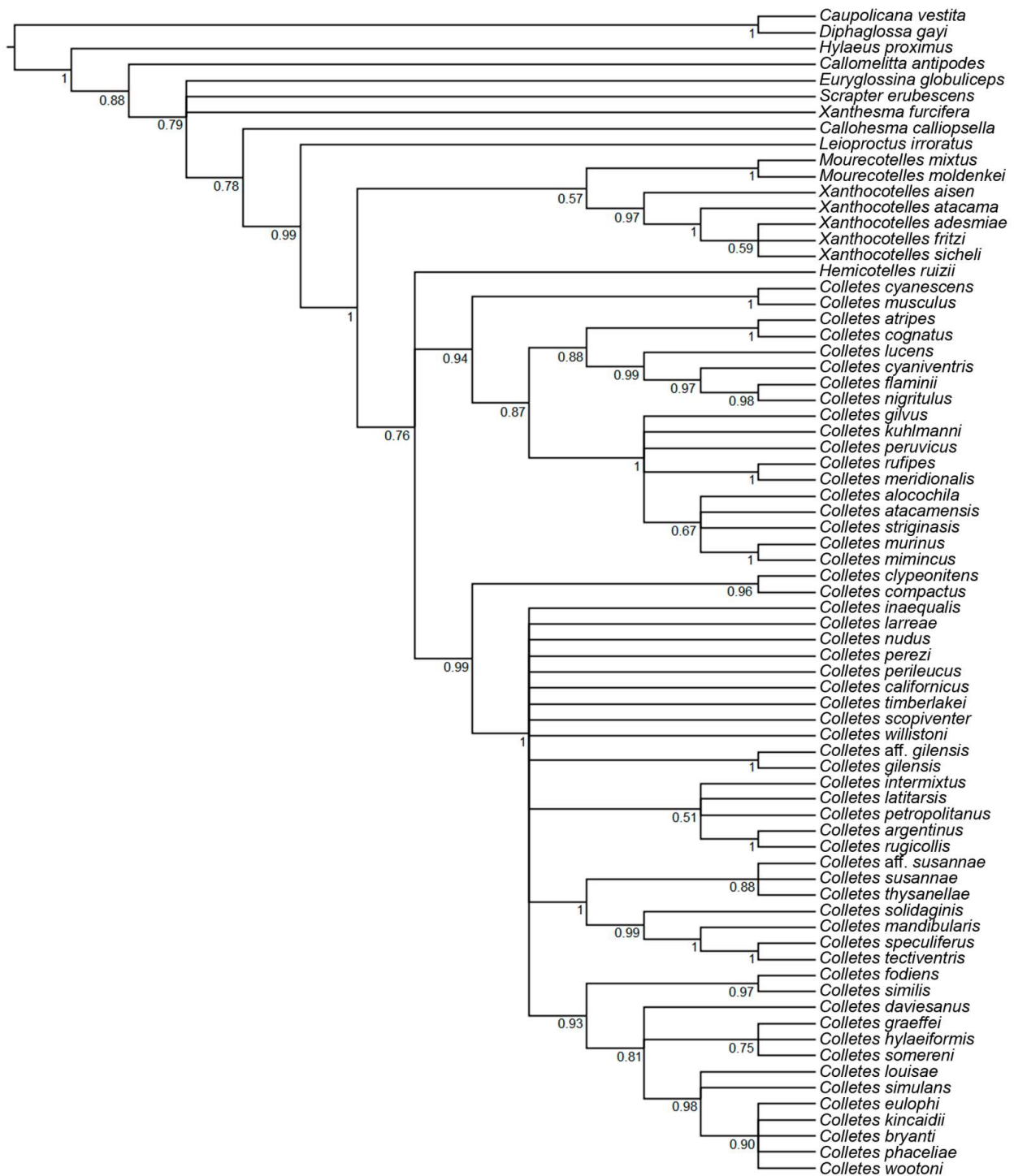
**Figure S2.** Bayesian tree obtained through analysis of the COI sequence data in MrBayes. Numbers below internal branches are posterior probabilities of the corresponding clades.



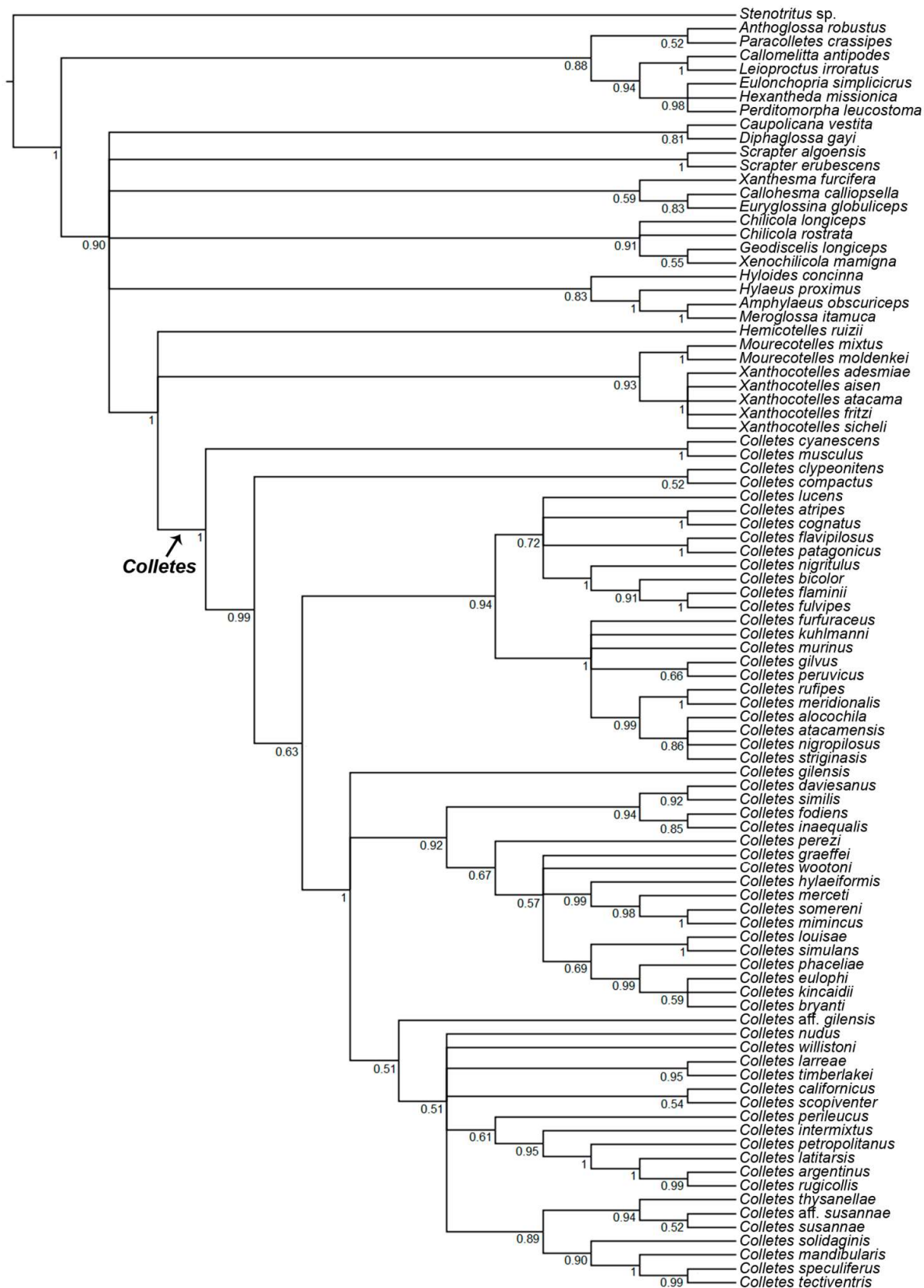
**Figure S3.** Bayesian tree obtained through analysis of the EF1a sequence data in MrBayes. Numbers below internal branches are posterior probabilities of the corresponding clades.



**Figure S4.** Bayesian tree obtained through analysis of the opsin sequence data in MrBayes. Numbers below internal branches are posterior probabilities of the corresponding clades.

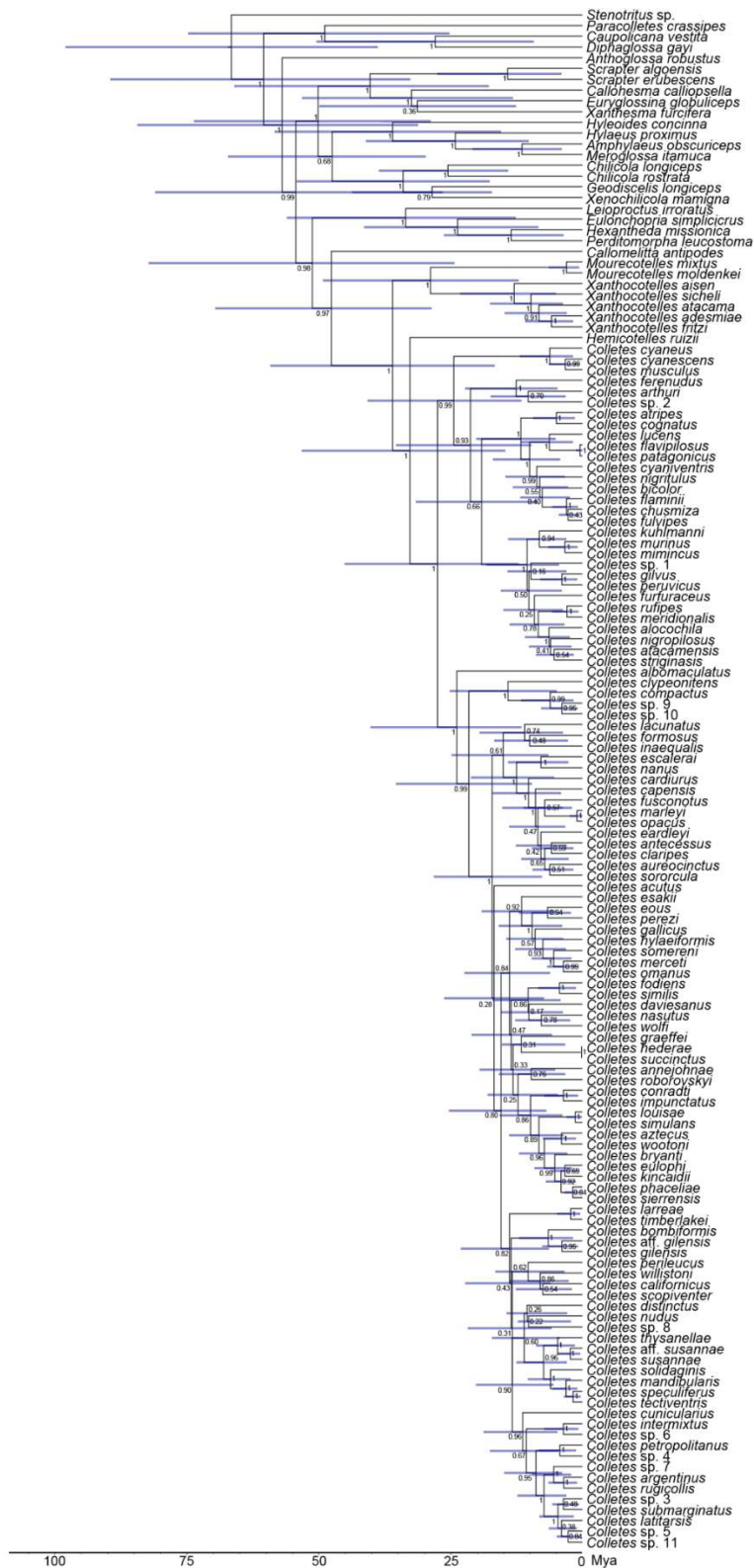


**Figure S5.** Bayesian tree obtained through analysis of pol II sequence data in MrBayes. Numbers below internal branches are posterior probabilities of the corresponding clades.



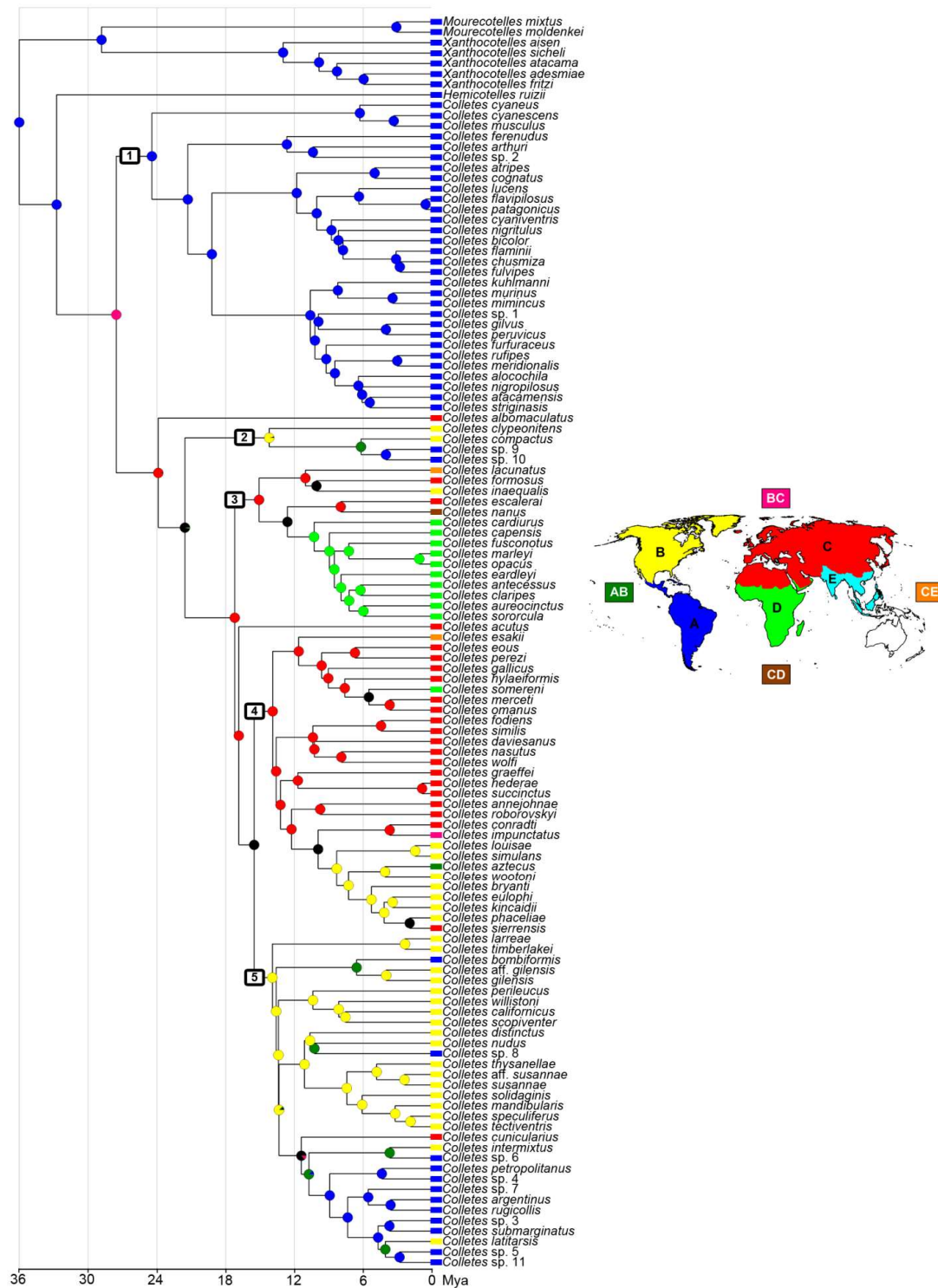
**Figure S6.** Bayesian tree obtained through analysis of the *wingless* sequence data in MrBayes. Numbers below internal branches are posterior probabilities of the corresponding clades.





**Figure S7.** Maximum credibility clade chronogram inferred through Bayesian phylogenetic analysis of the multilocus dataset in BEAST. Numbers adjacent to internodes are posterior probabilities of the corresponding clades. Blue bars depict height probability density at 95% of nodes.





**Figure S8.** Maximum clade credibility chronogram obtained through dated Bayesian analysis of the multilocus matrix in BEAST. Pie-charts depict ancestral geographic ranges of corresponding nodes inferred by the BioGeoBears analysis under the DIVA model in RASP. Boxes numbered from 1–5 indicate the five major clades of *Colletes*. All non-Colletinae taxa were pruned from the MCC tree. The five biogeographic areas (A–E) are illustrated on the map; polymorphic ranges are shown within rectangles.